ANNALS
OF
The Entomological Society of America

Volume XX DECEMBER, 1927 Number 4

SYMPOSIUM:—NEEDED LINES OF INVESTIGATION IN AMERICAN ENTOMOLOGY.

INTRODUCTION.

E. D. Ball.

The Science of Entomology has made wonderful strides in the past generation. The economic situation has been entirely rebuilt and changed from an empirical art to a scientific profession. The systematic side has prospered and gradually broadened until in many lines it rests upon a sound morphological and biological foundation. Man made catagories are rapidly being altered into the derived groups of a truly phylogenetic conception. The biological and ecological foundations are being laid and the work in the older fields of morphology and physiology revived. With that showing of progress research still needs much of stimulation and direction. Your committee evidently recognized this need in all lines and provided speakers for each phase. There are, however, other factors that are not specifically considered under these headings, and which possibly need the major emphasis at this time.

First.—What we need is not *more* research, as much as, better research—true research, if you please—research that seeks to ascertain the fundamental factors that control a given set of occurrences. We need that type of research that not only gets result, but explains the why and wherefore.

When an insect is rampant, it is research to work out an immediate method of destroying the pest, and that is the proper thing to do at the time, but if it stops there it is a relatively puny effort. It is like a man getting his firewood by cutting branches from a tree. The lowest branch may give him a little wood with a minimum of effort, much easier for the time being than cutting down the tree—each succeeding branch as he goes up the tree will, however, become more and more difficult, as he has no proper foundation from which to work and finally he will reach a point where the tree will have to come down. What

a saving of needless labor it would have been to have felled the tree in the beginning and hewed the branches from the prostrate trunk. Many of the branches, in fact, would have been broken off in the fall. So, it is in scientific research; to meet the immediate emergency, we chop off the nearest and most available branch and for the most part we have continued chopping branches of immediate control until the great problem before us today, is to bring down some of the solid trunks of biological principles. When we have an abundance of solid wood, we will find that the major portion of those branches are of no consequence at all.

When the mosquito bites you, the first thing to do is to slap; the next thing to go out and find the can in which she developed and kick it over, and keep on kicking until every can and breeding place in the surrounding region has been cleaned up. Thousands of generations, however, sat and slapped their lives away before anyone developed the energy to kick, and even today—there are many more slappers than kickers.

If there is an alarming and unusual outbreak of an insect, there must be some factor or more often factors responsible for the changed situation. A real research program will include a search for these controlling factors, and the particular variation that was at the time responsible for the upsetting of nature's balance. With these factors known, it will often be possible to anticipate an outbreak, and either prevent its occurrence or arrange in advance for effective control.

Take the codling moth as an example—this insect is world wide in distribution—a pest from the earliest cultivation of the apple, and still a major pest with many unknown factors. Nearly every experiment station in the apple belt had carried on investigations, but, how few of the hundreds of these investigations have made major contributions to the fundamental problem. There have been lots of slappers, and few kickers; lots of branch trimming and few trees felled.

This insect has two generations throughout the greater part of the commercial apple belt, and the behavior of these two generations varies widely, therefore, the best methods of controlling the two generations will vary as widely. This seriously complicates the problem, and yet, in spite of the knowledge of this situation 99% of the investigators instead of ascertaining its efficiency on each generation separately have been content to use the final results of the season's work, as a test of their methods. The first time the broods were separated, a cheaper and more effective method of control was developed, and yet, in trying to further improve this method, many of the investigators have gone back to the old practice of using the final results.

This reminds me of a man in the South last season, who sprayed his bean crop with calcium arsenate, nicotine sulphate, bordeaux mixture and derrisol, and succeeded in controlling the bean leafhopper. Now, he wants to know what to spray with this year. He controlled the hoppers, but he has four guesses as to what did it, and the writer after studying the situation carefully, has a fifth.

A considerable group of investigators representing three Government Bureaus, and two State Organizations, met the past year and worked out an elaborate and very complete program of investigation of a certain problem with reference to poisonous residues remaining on food products. The carrying out of this program involved a long series of spray tests, daily observations and records; a large number of samples taken and chemical analysis made, all of which were necessary to its solution. In the planning of this experiment, the very latest and most up-to-date knowledge of all phases of this subject was utilized—nothing left undone that could be anticipated as bearing on the completeness of the experiment. The work was done—a large amount of valuable data secured—and a goodly branch was hewed off the tree of entomological knowledge.

Soon after this work was completed, a single investigator, working in a crude laboratory, attacked one of the fundamental factors of this problem, and soon discovered that the spray used in this elaborate experiment was less than 50% as effective as another well-known compound for that particular work. By laying his axe to the root of a sapling instead of a branch of a big tree, that young man let a ray of permanent light into the gloom of the entomological woods.

The next step then, is to go back and do the big job over with the right compound—but is it? By that time let us hope the young man has tested the efficiency of different methods of application and, if, as is very likely to happen, he should find that a different method from the one employed gave 50% better results, then nothing would have been gained by the second effort, and yet, you must remember that the best available knowledge of both materials and methods was used in the planning of the experiment. When will we learn to do fundamentals first and applications afterward? Seventy-five percent of present expenditure of time and effort could be saved.

Second.—We need more cooperation—and again it is cooperation in working out basic facts that is needed. Fully 90% of our present cooperation is in eradication, quarantine, regulatory or reporting lines, and only a measly 10% is in lines that add to the sum total of our knowledge. If cooperation of the biologist, ecologist, physiologist and the economic entomologist went no further than to outline sound projects, it would accomplish wonders. If such a program had been in operation for the past ten years, one-half of the present activities would have "died a borning" as our grandmothers would have said.

The systematist should first study the limits of variation in a few species or a small group, and cooperate with the morphologist, the biologist and the student of distribution, in developing basic principles to be applied to the larger aggregates.

If this program had been followed in the past, there would be far less monographic misfortunes cluttering up our shelves and handicapping progress.

The writer recently worked over a genus that has been revised three times in the past few years, and decided that what it needs now is revision. The first reviser apparently did not know what a genus was;

the second was equally hazy on the limits of a species, while the third apparently had a supreme and child-like faith in the accuracy of the printed word—and none of these are characteristics of those whose works endure the ages.

Third.—We need more of the *Spirit of Research*—the inquiring mind—the spirit that subjects all statements to analysis before acceptance—the spirit that holds all truths as simply the best deductions from the evidence available but subject to modification at any time on the basis of new evidence. Such a spirit welcomes constructive criticisms and invites cooperation. Such a spirit grows and expands with the increasing knowledge and is ever young and up-to-date.

This is the day of mental tests, here is by far the best single test of the research mind that the writer has encountered. It was new to him, though doubtless old to many of you. It is a perfectly fair and complete statement of a simple problem without a sign of a catch or any play upon words. One need consider nothing except the problem involved.

"A man purchased a set of 12 volumes, each volume containing 200 pages or 100 leaves; each leaf one hundredth of an inch thick, so that each volumne, omitting extra pages and covers, was exactly one inch in thickness. He placed the 12 volumes on a shelf in a normal way, with volume 1 on the left, followed by volume 2, 3 and 4 to the right in regular order. Sometime later on examining them he found that a bookworm had eaten a hole in a straight line from page 1 of volume 1, to page 200 of volume 3. Omitting consideration of the extra pages and covers—how many inches of books did the worm eat through?"

Just take that home and try it on your graduate students—if they answer three, console them by telling them that there have been many others. If they answer one, or better yet, do not answer at all but get the books and see for themselves, rejoice, for you have the material on which to build.

Someone has said that the great scientific leaders of one generation, are not the sons, but the *students* of great leaders of the previous generation, and therefore, grand students and great grand students of the leaders of ages past. This raises no question of heredity, but asserts that the power to inspire with the research spirit and the wisdom to equip the growing mind with the fundamentals in principles and methods necessary to enable it to function efficiently is the gift supreme in the development of science.

It has been frequently noted that there is a marked difference in the ability to select and solve major problems manifested by students of different laboratories. If a fourth need in research were to be suggested, it would be to discover the human qualities that make for outstanding leadership in research, and possibly even more important, those rarer qualities that make for exceptional ability to attract and inspire research students. Because, be the need for research ever so great, in the last analysis it is upon the ability, equipment and inspiration of the research workers that the final outcome depends.

TAXONOMY.

By S. A. Rohwer,
Bureau of Entomology, Washington, D. C.

The taxonomic study of insects is the oldest and most fundamental line of investigation in all entomology, but it is evident from recent papers and reports of committees and from the general attitude of entomologists as a whole that it has not been so considered in recent years. You remember that at the last International Congress of Entomology[1], resolutions were passed pointing out the importance of taxonomic work and recommending that universities recognize its value and consider theses on taxonomy worthy of merit. At a recent symposium held in London[2] there was a long discussion about the value of taxonomic work. Prior to that, taxonomy and its relation to other lines of investigation had been discussed by retiring presidents[3] and at symposiums[4] before other societies. All this agitation about taxonomic investigations evidently shows either that there is something the matter with the taxonomic work that has been done, or that so few people have entered this field that their work is not covering the ground adequately. In any event we may feel certain that the science of taxonomic entomology needs to be overhauled to some extent. I am not an accurate enough diagnostician to point out all of the sore spots, but in the following remarks I shall try to indicate some places where improvement can be made. Some of the points I wish to emphasize have already been brought to your attention by Dr. Howard[5] in his admirable address two years ago, and I recommend that you reread this address periodically for stimulation and suggestions. Some of these and other points now suggested have been mentioned by others, but a repetition may emphasize their importance.

The subject of this symposium calls, if I interpret it correctly, for definite suggestions as to where taxonomic investigations are needed at present, and perhaps it is well that it has been so limited. But if I were to confine myself to this alone I should either be through when I had said that taxonomic investigations are needed in all groups of insects, or else I could read you a list of the groups of insects and set you all to wondering whose scheme of classification I was using, and cause you to lose sight of the main object of the symposium. I know of no group of American insects which is sufficiently well studied to form a model unit, on which further investigations are not needed.

---

[1]The Third International Congress of Entomology (Zurich), July, 1925. These resolutions are republished on pages 476 and 477, in reference given in footnote 2.

[2]See Annals of Applied Biology, vol. 13, no. 3, August, 1926, pp. 466-485.

[3]Gahan, A. B. Proc. Ent. Soc. Wash., vol. 25, no. 3, March, 1925, pp. 69-78.

[4]Rohwer, S. A., Baker, A. C., and Ball, E. D., Jour. Wash. Acad. Sci., vol. 16, no. 3, Feb. 4, 1926, pp. 53-67.

[5]Howard, L. O., Annals Ent. Soc. America, vol. 18, no. 1, March, 1925. Republished in Ann. Rept. Smithsonian Inst., 1925, pp. 355-372.

It has been pointedly said by a well-known student of insect taxonomy that the best way to find out how little you know about a given group is to "revise" it, and that the influx of material following publication will convince you that the revision itself needs revision.

With this in mind, I shall present as an introduction, to what seem to me to be some of the more pressing taxonomic problems, some of the needs of taxonomic work as a whole.

Before attempting to outline these needs, may I first set forth the object of taxonomic work as I see it? Briefly, it is the arrangement of insects in a phylogenetic sequence based on a knowledge of their morphology, ecology, physiology, and development, and it should thus include the idea that a species is an aggregation of *living* individuals which in nature react in a more or less uniform manner to the same stimuli. For the present, at least, I think we must assume that similar reactions to the same stimuli cause the development of similar characters and characteristics, and therefore that we can best continue to base our classifications on morphological differences. We should not, however, overstress or misinterpret morphology. Striking morphological differences or similarities may not be the real key to relationships. When morphology is properly interpreted, however, I feel sure that we will find that the sequence produced by such interpretation will harmonize with the arrangements based on an analysis of the ecology, physiology, and development. No taxonomic study should be undertaken without a realization of the importance of development and of relation to environment.

Perhaps 80 per cent of all the taxonomic work on American insects has been done by amateurs, or people who have classified insects as a hobby. To these students entomology, and especially that type of entomology which until recently has been called "economic entomology," is greatly indebted. Without their aid "economic entomology" would have been greatly hampered, and I do not wish in any way to belittle their achievements. I do feel, however, that the time has come when we must have a more profound respect for taxonomy and look to the building up of a corps of professional taxonomists. The science of the classification of insects has become so vast, there are so many forms already described, and so many of the species have an extensive distribution, that it is unsafe and inadvisable for us to continue to encourage taxonomic investigations by people who do not have access to large collections and large libraries. Taxonomic work in the futue must be founded on abundant material collected over a wide area. Groups must be studied from the standpoint, not of a limited region, but of continents, and, better yet, the world as a whole. So much has already been done in many groups that it is practically impossible for private individuals to obtain all of the literature, and I therefore feel that the day of the amateur taxonomist is—and justly so—rapidly passing. It is no longer desirable to consider as taxonomy the sorting of specimens on the bases of minor differences. The early workers were justified in doing this, but a deeper study must now be made.

If taxonomic entomology has not large openings for amateurs, and if we insist that it must be based on more intensive studies, then we must expect and demand that the workers entering into this line of investigation be more broadly and thoroughly trained than they have been in the past. They must have a keen appreciation of the underlying laws of nature which permit an understanding of phylogenetic development. They must be well versed in those sciences which are handmaidens to taxonomy, such as morphology, cytology, embryology, and paleontology, and they must not forget the need of an appreciation of the fundamentals of geographical distribution. The taxonomist of the future, therefore, must be well and broadly trained. He must be able to recognize that his science, and the good that he does to science as a whole, will depend to a large extent on his ability to keep pace with the work that is done in other fields and to coordinate this work with his. Furthermore, he must use the results obtained from these other investigations and incorporate them into his publications. A knowledge of the few sciences mentioned above is not sufficient. Many of us are quite aware of the present tendency on the part of certain workers to apply mathematics to taxonomic studies; and while some of us fail to see the application of mathematics to all phases of taxonomic problems, we must admit that in many places it has a decided usefulness.

If the estimate that there are at least 640,000 kinds of described insects is correct, and if we concede that ultimately approximately 5,000,000 species of insects will be known in the world, we may be somewhat appalled at the number of forms that should be described to make our knowledge complete. Those who have been describing so many hundred new species each year may feel proud and to some extent satisfied that they are doing their bit to help catalogue the world's insects. To some extent I can sympathize with them. Years ago I used to look with considerable pleasure on a new species. Now I am quite sure that for the good of the cause the time of "scouting" in taxonomic entomology is past. Instead of describing so many more new species, we should devote more effort to coordinating and summarizing what is known about those already described. Although papers containing only miscellaneous descriptions are necessary, I have scant respect for them. I have, on the other hand, the highest regard for those papers which are of a revisionary nature. Theses which review what has been done, coordinate it, and augment it by a study of all the additional material the writer can examine, hold promise of being real contributions.

May I emphasize this by an illustration? I do not believe that one is contributing much to the science merely by just describing another *Halictus* when there are already probably six or seven hundred described from all the zoogeographic regions, and when many of these cannot be recognized from descriptions. It would be a comparatively simple matter to sit down and prepare descriptions, without any great danger of making synonyms, for probably 40 or 50 new species of Halictus occurring in North America. To do so would only be making

more difficult the work of our successors. The only satisfactory way to treat the *Halictus* of North America is to coordinate those species which have been characterized with those not characterized, and make a comprehensive revisionary paper which will not only clearly set forth the distinguishing characters of the species, but will give us some definite knowledge as to the distribution and seasonal occurrence of those which are described. If I am correct that this "scouting" in taxonomy is no longer justified, and you all agree with me, we will not have any more of those interesting competitive experiences that have existed in the past, when the workers have hastened to describe new species in order that the types might be in their collections or their museums. And that is not all, for could we eliminate the selfish competition we could then develop much more that necessary adjunct to all scientific endeavor, cooperation.

In most lines of entomological investigation, as well as in many of the other sciences where the largest advances are made, there have been cooperation and coordination of work, and not just a hit-or-miss idea of sorting and arranging certain facts. Taxonomic investigations have not been coordinated, and I am sorry to say that cooperation is only beginning to manifest itself. Duplication of effort in taxonomic work is often appalling. Within the last 18 months I have known of six students who wished to undertake revisionary studies on the fleas of North America. Each one of these individuals had devoted considerable effort to building up a local collection, and gathering together literature and a bibliography. Any one of these workers would gladly have devoted the same amount of preliminary effort to gathering materials on another group. A freer cooperation between those directing or suggesting problems would have at least discouraged this duplication of effort. Some clearing house where records could be kept of taxonomic problems undertaken, and perhaps a periodic bulletin telling others of these investigations and giving information on recent collections of insects, would be of considerable help and might prevent duplication of effort and stimulate cooperation.

Most of the work that has been done in the past on the classification of insects has dealt with the adults. Our classifications are all based on characters selected from the adults, and only recently has any effort been made to study in a comprehensive way the immature stages. With practically all insects the injurious stage is that of the larva or nymph, and I believe that it is extremely important that investigations be made into the classification of the immature stages of all orders. The need for investigation of the immature stages stands out most strikingly, however, in those groups in which the metamorphosis is complete. There is very little resemblance between the caterpillar and the moth, yet there is sufficient resemblance between the nymph and the adult grasshopper to permit in many cases a definite association of characters. The type of work that is being done by Malloch and Greene in Diptera; by Hamilton, Craighead, Richmond, Böving, St. George, Champlain, Wood, Cotton, and others, in Coleoptera; the studies of Dyar, Forbes, Mosher, and Heinrich in Lepidoptera; and

those of Yuasa, McGillivray, Parker, and Middleton in Hymenoptera, have gone a long way in the right direction. Still we have only scratched the surface. Valuable hints on phylogeny, necessary information as to how to recognize those stages which are injurious, will be gained by the comprehensive study of the immature stages. While we will all agree that we should make studies on the immature stages, I do not believe that many of us have cooperated towards making these studies possible. The study of the immature stages must be preceded by the amassing of material. Without definitely associated larvæ and adults, more harm than good may be done by attempting to do much work on the immature stages. Every one of us can render great service by preserving immature stages which can definitely be associated with adults. The insect collection in the U. S. National Museum is outstanding in the quantity of material of immature stages it contains, and yet we are finding that this is woefully inadequate to carry on the types of studies which we wish to make.

The study of the immature stages is such an outstanding needed line of investigation and offers so much of practical value that it seems advisable to add a word of caution lest investigators in this field lose sight of the whole. A study of the immature forms alone may be likened to a study of only a part of the organism. Our classifications should be built on a study of the whole insect, its structure, behavior, and history. The magnitude of the task offers some practical difficulties in treating the whole problem in one publication, but the investigator should not lose sight of the desired result.

The subject of our symposium limits our discussion to the needed lines of investigation in American entomology. But this is hardly fair to taxonomy, for the specialist who attempts to confine his studies to American insects will not be rendering the fullest service. Man and his civilization have moved and are moving many insects. Some of these have found and may again find access to our country. A prompt recognition of these is of great importance to man, his crops, and his animals. Who is going to safeguard us from these unwelcome enemies if the taxonomist confines his studies to native insects? The taxonomist must have a world viewpoint, and as the work progresses and we appreciate more the principles outlined above it is hoped that taxonomic work will have a much broader outlook and be world-wide in scope.

Those of you who have done real taxonomic work are undoubtedly familiar with many of the perplexing problems which confront the taxonomist. What are the limits of variation in a species? What characters may be relied on? Is a certain difference caused by the host or does it represent the effect of a particular region? These and many more questions confront the taxonomist every day. How can they be solved? Will the study of large series from widely separated regions and reared from a number of hosts furnish the answer? Yes, such a study will help! But another plan which would furnish a more satisfactory answer would be to study the progeny of known parents. Careful rearing of specimens of known pedigree on a number of hosts and under a wide range of ecological conditions would help immensely.

Experiments of this kind conducted on a few forms would furnish some criterion which would aid in solving the same problem as it occurred in other groups. Could not some graduate students rear and make critical analysis of the variation in the progeny of known parents? Such a study offers ample opportunity to test one's ability to do independent research and would undoubtedly offer abundant test of one's initiative.

Looking over the groups of insects which are badly in need of revision, I have selected only a few examples, and as I read the list you will undoubtedly note that I have chosen mostly those groups which have a direct bearing on American agriculture. This is not because the other groups do not require study but because the need of revisionary work on the economically important groups is being constantly impressed upon me and also because it is necessary first to investigate those things which affect our own welfare.

In the Coleoptera we need comprehensive revisionary work in the following families: Scarabaeidæ, Chrysomelidæ, Coccinellidæ, Scolytidæ, Cerambycidæ, Buprestidæ, and Curculionidæ. In Lepidoptera the Pyralidæ, Noctuidæ, and Geometridæ might be the first groups to be considered; in Hemiptera, the Miridæ and Jassoidea; in Diptera, the Tachinoidea and Trypetidæ; in Orthoptera, the Acrididæ; in Hymenoptera, the parastic forms and the sawflies; in ectoparasites, the parasitic mites, especially those of the genus *Sarcoptes*.

I have mentioned only a very few of the lines of investigation in taxonomic entomology and have made no effort to outline these in detail or to defend the investigation suggested. The outlining of abundant problems in taxonomy would be easy and it would be almost as easy to set forth arguments why the investigation should be done. But neither of these has a place at this symposium. Furthermore, all taxonomists know where and how to start a problem and they all realize that a satisfactory detailed outline cannot be followed. Only a general outline can be prepared, for as the work progresses the details have to be modified to suit the needs and the material available.

I hope I have succeeded in pointing out enough places where investigation is needed to convince you that the field of entomological taxonomy offers wonderful opportunities. I trust that I have been more successful and have conveyed to you the impression that the need for investigation into the classification of insects exists in all the major units and that there are problems enough to keep hundreds of workers busy for years to come. To describe all the kinds of insects which will eventually be known in the world will take, at the present rate, over five hundred years.

But that is not all I hope for. I am anxious that you gather some of my desire to make the taxonomic work of the future more thorough, more comprehensive, and thus more useful. If I have been successful in this, we can all cooperate and make the taxonomic work on insects in America more efficient and bring to it the much needed facilities for publication and indexing of the work of others. And more than that, we can obtain more and better-trained workers, larger collections, and better laboratories in which these new investigators may study.

INSECT PHYSIOLOGY.

PAUL S. WELCH,
University of Michigan.

INTRODUCTION.

Insect Physiology, by the nature of its content, does not lend itself readily to geographical distinctions. Hence my contribution to this discussion will contain little that is characteristically American in its bearing. As a subscience, the physiology of insects stands at the threshold of its development despite numerous scattering, physiological investigations of the past which have used insects as material. One seeks long, perhaps in vain, to find any aspect of the subject which would not, on scrutiny, yield opportunities for extensive contributions to our knowledge. Hence my task is one of choosing *what* to discuss. In these days of vigorous research one finds his own field of intimate knowledge hemmed in by increasingly extensive expanses of outlying territory which must of necessity be known but dimly and from a distance. I have assumed, therefore, that our subject does not imply necessity of a complete survey of the assigned field; that if my discussion concerns itself with research opportunities which have appeared directly or indirectly from my own investigations and about which I can perhaps claim some slight knowledge, I will approximate the expectation of those who planned this program.

Since at present I am investigating certain aspects of insect respiration, I shall use that subject as the entering wedge.

RESPIRATION.

Respiration in insects has long intrigued the interest of investigators. Its fundamental role in the maintenance of life, the innumerable modifications of accessory organs, the versatility of insects in utilizing direct and indirect sources of oxygen supply, the intimate relation of respiration to economic problems—all these have done much to direct attention to this field. Nevertheless, the subject deserves intensive study at the present time.

Functions of Organs.

As is often the case, morphology has here led far in advance of physiology. Functions of some well known organs are imperfectly known and differences of opinion common. Indeed, the conclusion that certain organs function in respiration at all is apparently inferential. (Example: Ventral eversible sacs of Thysanura, Perla, and Scolopendrella; recent expressions of doubt (Remy, 1925) as to respiratory function). The existence of inspiratory and expiratory spiracles is still questioned although the most recent work (Lee, 1925; Wrede, 1926) seems to show a certain agreement. Whether unharmonious results are due to faulty experimentation or whether they arise from the use

of different species and different life history stages, only future research will tell. Many other similar cases might be cited. A series of critical experimental investigations involving a wide range of species must be made before our knowledge will begin to take on a dependable form.

Reduced Organs.

That the truly apneustic and holopneustic types of tracheation are connected by many forms of intergrade (sometimes grouped under the term Hemipneustic) is common knowledge. The degree of reduction of both spiracles and tracheae is, in different insects, a matter of great variation and the line of demarkation between the two types is elusive. I have long doubted the truth of some current actual or implied statements, that reduced spiracles and tracheae are either functionless or ineffective. The case is easily settled where it can be shown that there is complete, unqualified morphological closure, but anything short of this is worthy of critical investigation. Takatsuki postulated waxy secretions in the tracheae of mosquito larvae which act as barriers but Hacker (1925) failed to confirm these results.

Reduction of the whole or a part of a tracheal system does not necessarily preclude functioning (Welch, 1922). It may result in spiracles and tracheae no smaller than those of some minute holopneustic insects. Furthermore, it has been shown (Krogh, 1920a, 1920b) that there is no difficulty in the ventilation of such a system since diffusion alone is an effective factor in tracheae of extremely small diameters. The whole question of apneustic, and hemipneustic tracheation, must be reapproached by means of modern morphological and experimental methods.

Function of "Gills."

Time honored conceptions concerning the functions of certain organs, have too long escaped modern scrutiny. Various adaptive organs of aquatic insects are thought to be respiratory and often called gills. Conceding that undoubtedly some are true gills, others need re-examination. Fox (1921) claims to have shown that in a red Chironomus larva no more oxygen is absorbed by the anal gills than by the general body surface and "no oxygen at all absorbed by the ventral gills." Here is a direct challenge to a very common interpretation of long standing and likewise a tacit interrogation as to other similar structures. So far as I have been able to discover, no one has repeated or extended Fox's work. Remy (1925) in his large work on respiration in invertebrates makes use of a number of insects, including Chironomus larvae. Unfortunately his method failed at this particular point and no definite results were obtained. He makes no mention of the work of Fox.

Suspicion has also fallen upon the role played by tracheal gills. Cuenot (1925) claims, on the basis of experiments on naiads of Ephemerida and Odonata, that either these organs do not function in respiration at all, or at best are minor adjuncts to other more important receptors of dissolved oxygen. Remy (1925), however, gives them a higher rating.

Carbon Dioxide Elimination.

The method of carbon dioxide elimination has long been a matter of disagreement. Krogh (1913) and others have held that in certain insects CO_2 must be eliminated by means other than the tracheae, while Buddenbrock and Rohr (1922), Lee (1925) and Wrede (1926) present evidence to show that the tracheae are the avenues of elimination. Dewitz (1890), Muttkowski (1920), Lee (1925) and others have demonstrated the possibility of CO_2 diffusion through the integument but the degree to which it actually takes place in the living insect is still a matter of uncertainity. The occurrence of calcium carbonate in the Malpighian tubules and the fat-body (Imms, 1925) has been thought by some to be due to the neutralization of some of the CO_2 in the blood, although proof seems to be lacking.

Anaerobic Respiration.

The existence of insects, as well as certain other animals, in the bottom of deep inland lakes under conditions of complete absence of dissolved oxygen, (summer and winter stagnation periods), is a well established fact. The same ability to thrive in the absence of free oxygen seems to be true of many internal parasites. The source of the oxygen required in the internal metabolic processes is unknown. Intramolecular respiration has been postulated; catalase determinations have been made; chemical methods of increasing resistance to reduced dissolved oxygen have been tried; and Cole (1921) claims that minute amounts of an oxidizing substance formed in decomposition of plant tissue under oxygenless conditions may possibly be atomic oxygen which might serve as the oxygen supply for these insects. The problem still awaits solution.

Other Problems in Respiration.

(1) Sources and roles of gases, particularly those in the tracheal system sometimes referred to in the literature as Air of Transformation (Muttkowski, 1920) are still more or less of an enigma. Keilin (1924), observing that in aquatic apneustic insects on hatching or emerging from a moult have the tracheal system first filled with fluid, then by a gas, holds that the former is absorbed by surrounding cells and the space thus vacated immediately filled by gases diffusing from the blood. "Internal and external inflation" gases still remain unsolved. Likewise, those gas accumulations which appear in certain aquatic insects on prolonged exposure to slightly unfavorable conditions are yet to be explained.

(2) Differences in oxygen requirements constitute a subject of uncertain status. Gill area, gill number, or gill absence can not be taken as dependable criteria of oxygen demand. Dodds and Hisaw (1924) found a definite correlation between gill area and oxygen content in certain Rocky Mountain mayfly naiads, but on the other hand numerous opposing examples prevail, as for example, the larvæ of two closely allied of the genus *Nymphula* (Lepidoptera) both living in the

same environment (Welch, 1916; 1922) both of same body size, but one with more than 400 gill filaments, and the other with none at all. Entomological literature contains mis-statements, direct or implied, as to the supposed limiting effect of oxygen supply. A much repeated one explains the universal restriction of *Simulium* larvae to running water because that water alone has a sufficiently high dissolved oxygen content to meet the high oxygen requirement of the larvae, when as a matter of fact, the idea is fallacious as shown by the unpublished work of one of my graduate students.

The next subject naturally follows in the wake of a respiration discussion.

Insect Blood.

Investigations on the morphology and physiology of insect blood are specially urgent because of the recent opening up of at least two seemingly prolific fields.

(1) Respiratory pigments or proteins.

The older idea of the complete independence of circulation and respiration in insects is toppling, due to recently reported evidences (Muttkowski, (1921a, b, c); Keilin 1925) of chemical substances in the blood and elsewhere which are thought to perform a function similar to that of haemoglobin. Haemoglobin has long been known in a few insects, but the indication that other oxygen carrying substances may occur widely throughout the insect group puts a new face on the whole respiration problem and blocks out a field of investigation which may have important possibilities. Remy (1925) found evidence that the "young leucocytes" in contact with the tracheoles fix oxygen and distribute it to the different tissues; also that the blood plasma may play a similar but lesser role. His method, however, was not designed to identify oxygen carrying substances.

(2) Physical changes in Haemolymph. In this second field a single paper has brought to light possibilities which may be far reaching. Ackerman (1926) working on the problem of the physiological basis of wing production in aphids, found, among other things, that the haemolymph contains four kinds of globules, two pigmented and two colorless lipoid ones; that reduced temperatures cause the lipoid globules to solidify; that both wing production and the solidfication of the fat globules appear to be dependent upon the breaking of the delicate, unstable brown globules; and "that wing production is dependent upon the proportion or concentration of certain substances in the haemolymph as brought to pass by the rupture of the brown globules." This distinctly new point of attack has application more far reaching than the mere problem of wing production in aphids. Even if perchance future research should fail to confirm Ackerman's explanation of wing production, there would still remain his fundamental findings of physical changes in the haemolymph, their interrelations, and their correlation with environmental changes. May it not be that other internal events in insects are concerned in these phenomena. May they not have some fundamental relation to problems of metamorphosis and development,

growth, polymorphism, and nutrition. And do not these findings possibly clear the way for a better understanding of temperature change effects in insects.

Nutritional Problems.

Out of the array of possible nutritional problems only two are mentioned.

(1) Influences of Associated Organisms:—For a long time it has been recognized by many investigators that internal symbionts may play some important role in the digestion of food stuffs normally taken by the host insect. The work of Cleveland (1924, 1925 a, b, c) has opened the way to a whole series of needed investigations. By the development of promising methods (the removal of the symbionts by means of certain temperatures, by starvation, and by oxygenation), he has apparently solved the approach to a dependable experimental study of the relation of various micro-organisms to their hosts. Many insects other than termites make some use of woody materials and the extent to which cellulose is available as food can now be investigated. Possibly other forms of digestion are related to the presence of micro-organisms and the same or similar methods may facilitate future investigations.

(2) Dissolved organic matter.—Some years ago Pütter (1907 a, b) proposed that the dissolved organic matter in the water must serve as food supply for aquatic organisms, and by several subsequent investigations appeared to show that many kinds of animals, including Arthropods, make extensive use of these materials by direct absorption. In some cases he got surprisingly large percentages of the nutrition secured in this way. From the outset, Pütter's contention fell, and still falls, upon skeptical ears. Recently, seeming confirmation of his results appears in the work of Esaki (1926) and Krizenecky, and Podhradsky (1924) working with amphibian larvæ. On the other hand, Dakin (1925) performed experiments similar to those of Pütter but with negative results. One of the several objections raised against Pütter's findings hinges upon the actual amount of this dissolved organic matter in the water. Pütter found high values in sea water; other workers (Moore et al., 1912) claimed the presence of no more than one part in one million of soluble material. The whole question has been reopened and given a new importance by the recent work of Birge and Juday and their co-workers (1926) which shows that in Wisconsin lakes the dissolved organic matter is far greater in quantity than in sea water; that it is "ordinarily several times and often many times greater than that in the plankton;" and that "it is as well suited for food as is the organic matter of the plankton" itself. Again the controverted question—to what extent is it actually used directly as food by the various aquatic animals. This is, of course, a problem of wide biological ramifications, but since a great many insects live partly or wholly submerged in aquatic environments, questions relating to the direct availability of dissolved organic foods are equally pertinent to our subject. It is still an open field and merits the attention of investigators.

Body Surface Features.

Notwithstanding numerous scattering papers which deal with the relation of external surface features of insects to surface tension phenomena, one who needs certain kinds of fundamental information as to the chemical or physical bases which lie back of the ways in which liquids relate themselves to body surface, pubescences, and etc. will likely meet with some disappointment. The recent paper by Hacker (1925) presents, among other things, interesting and valuable data on the role played by differential wetting in the life history of mosquito larvae and in their susceptibility to the effects of oil. Much remains to be learned as to why certain liquids wet certain substances; why varying degrees of wetting occur in insect structures; and why the hydrofuge character of some surfaces may be more permanent than others. Body hairs, whose tips are wetable and whose bases are hydrofuge have been postulated to help explain certain respiration phenomena in aquatic insects. The very obvious bearings of this subject on problems in insect respiration, insect habits and insect control measures, not to mention other possible applications, make necessary an extension of our knowledge in this direction.

Hydrogen ion Concentration.

Finally, I refer to the role of hydrogen ion concentration in insect biology. For some reason insects have functioned too little in the numerous pH investigations of recent years. Aside from papers dealing with its relation to mosquito larvæ, one searches with restricted success in the literature for specific information on other forms. In fact, the intrinsic value of pH as a single influence is occasionally denied (Hyman, 1925). If anything convincing is to come out of the contention that pH has a specific action on insects, more work must be done in the future. Likewise, its role in the internal processes of insects is still in an unsatisfactory state.

LITERATURE CITED.

Ackerman, L. 1926. The Physiological Basis of Wing Production in the Grain Aphid. Journ. Exp. Zool., 44:1-61.

Birge, E. A. and **Chancey, Juday.** 1926. The Organic Content of Lake Water. Proc. Nat. Acad. Sci., 12:515-519.

Buddenbrock, W. V. and **Rohr, G. v.** 1922. Über die Ausatmung der Kohlensäure bei Luftatmenden Wasserinsekten. Pflügers Archiv ges Physiol. d. Menschen u. d. Tiere, 194:218-223.

Cleveland, L. R. 1924. The Physiological and Symbiotic Relationships between the Intestinal Protozoa of Termites and their Host, with special Reference to Reticulitermes flavipes Kollar. Biol. Bull., 46:177-225.

1925a. The Ability of Termites to live perhaps indefinitely on a Diet of Pure Cellulose. Biol. Bull., 48:289-293.

1925b. The Feeding Habit of Termite Castes and its Relation to their Intestinal Flagellates. Biol. Bull., 48:295-308. 1 pl.

1925c. The Effects of Oxygenation and Starvation on the Symbiosis between the Termite, Termopsis, and its Intestinal Flagellates. Biol. Bull., 48:309-326. 1 pl.

Cole, A. E. 1921. Oxygen Supply of certain Animals living in Water containing no Dissolved Oxygen. Journ. Exp. Zool., 33:293-320. 2 figs.

Cuenot, L. 1925. L'Adaptation. Paris. 420 pp.

Dakin, W. J. and **Dakin, C. M. G.** 1925. The Oxygen Requirements of certain aquatic Animals and its bearing upon the Source of Food Supply. Brit. Journ. Exp. Biol., 2:293-322.

Dewitz, H. 1890. Einige Beobachtungen betreffend das geschlossene Tracheensystem bei Insekten larven. Zool. Anz, 13:500-504; 525-531.

Dodds, G. S. and **Hisaw, F. L.** 1924. Ecological Studies of Aquatic Insects. II. Size of Respiratory Organs in Relation to Environmental Conditions. Ecology, 5:262-271.

Esaki, S. 1926. The Feeding of Amphibian Larvae with Various Nutritive Substances given in Water or with Other Solutions. Folia Anat. Jap., 4, no. 1.

Fox, H. M. 1921. Methods of Studying the Respiratory Exchange in small aquatic Organisms, with particular Reference to the Use of Flagellates as an Indicator for Oxygen Consumption. Journ. Gen. Physiol., 3:565-573. 5 figs.

Hacker, H. P. 1925. How Oil kills Anopholine Larvae. F. M. S. Malaria Bureau Reports, 3:1-62. 2 pls., 6 figs.

Hyman, L. H. 1925. On the Action of certain Substances on Oxygen Consumption. Biol. Bull., 49:288-322.

Imms, A. D. 1925. A General Textbook of Entomology. London, 698 pp.

Keilin, D. 1924. On the Appearance of Gas in the Tracheae of Insects. Proc. Cambr. Philosoph. Soc., (Biol. Sci.), 1:63-70.

1925. On Cytochrome, a Respiratory Pigment common to Animals, Yeast and Higher Plants. Proc. R. Soc., Biol. Sci., Series B, 98:312-339.

Krizenecky, J. and **Podhradsky, J.** 1924. Studien über die Funktion der im Wasser gelösten Nährasubstanzen im Stoffwechsel der Wassertiere. I, II, III, IV Mitt. Pflügers Archiv ges. Physiol. d. Menschen u. d. Tiere, 203: 129-140; 204:1-24, 25-41, 471-476.

Krogh, A. 1913. On the Composition of the Air in the Tracheal System of some Insects. Skand. Arch. Physiol., 29:29-36.

1920a. Studien über Tracheenrespiration. II. Über Gas-diffusion in den Tracheen. Pflügers Archiv. ges. Physiol. d. Menschen u. d. Tiere, 179:95-112. 5 figs.

1920b. Studien über Tracheenrespiration. III. Die Kombination von mechanischer Venti,ation mit Gasdiffusion nach Versuch an Dytiscuslarven. Pflügers Archiv ges. Physiol. d. Menschen u. d. Tiere, 179:113-120. 2 figs.

Lee, M. O. 1925. On the Mechanism of Respiration in certain Orthoptera. Journ. Exp. Zool., 41:125-154.

Moore, B., Edie, E. D., Whiteley, E. and **Dakin, W. J.** 1912. The Nutrition and Metabolism of Marine Animals in Relationship to (a) Dissolved Organic Matter, and (b) Particulate Organic Matter of Sea-water. Biochem. Journ., 6:255-297.

Muttkowski, R. A. 1920. The Respiration of Aquatic Insects. Bull. Brook. Ent. Soc., 15:89-96.

1921a. Copper in Animals and Plants. Science (n. s.), 53:453-454.

1921b. Studies on the Respiration of Insects. I. The Gases and Respiratory Proteins of Insect Blood. Ann. Ent. Soc. Am., 14:150-156.

1921c. Copper: Its Occurrence and Role in Insects and Other Animals. Trans. Am. Micr. Soc., 40:144-157.

Putter, A. 1907a. Die Ernährung der Wassertiere. Zeit. f. allg. Physiol., 7:283-320.

1907b. Der Stoffhaushalt des Meeres. Zeit. f. allg. Physiol., 7:321-368.

Remy, Paul. 1925. Contribution à l'étude de l'appareil respiratoire et de la respiration chez quelques Invertébrés, Nancy. 222 pp. 8 pl.

Welch, P. S. 1916. Contribution to the Biology of Certain Aquatic Lepidoptera. Ann. Ent. Soc. Am., 9:159-190. 3 pl.
1922. The Respiratory Mechanism in certain Aquatic Lepidoptera. Trans. Am. Micr. Soc., 41:29-50. 2 pl.

Wrede, F. 1926. Beiträge zur Atmung der Insekten. I. Mitt. Über die Tracheenatmung bei Raupen (Harpyia vinula und Sphinx Ligustri). Pflügers Arch f. d. ges. Physiol. d. Menschen u. d. Tiere, 211:228-243.

INSECT BIONOMICS.

R. W. Doane,
Stanford University.

The term bionomics, first suggested by Gedder many years ago, means, literally, life and order, or custom, in other words, the science of life or living things. Certainly a broad enough subject for a ten or fifteen minute discussion. All of the other subjects suggested for this symposium might very well be included under the general heading of bionomics; so the only limit I could see to the field I might cover in this discussion is the time limit and the topics suggested for the other writers.

Insects probably first interested primitive man on account of their presence on his body where they interfered, more or less, with his peace and his comfort. Then began the study of methods of insect control—economic entomology, if you please. At least one of the control of methods developed at that time, or even earlier, is still in use and may be observed at almost any time when one visits the anthopological cages in our zoological parks. In more civilized communities this method is modified somewhat in as much as the fingernails, instead of the teeth, are used for crushing the prey.

Early man soon noticed that some of these pests seemed to confine their attention to the head of the victim, hiding away, when not busy, in the long shaggy locks, as other beasts of prey would hide away in the thick forest glades. Others were more common on other parts of the body, taking refuge, when disturbed, in the folds or crude seams of the primitive clothing. These two forms looked alike but their habits were somewhat different and the question soon arose as to whether they were really the same kind or different kinds of pests. So the study of Taxonomy arose and from that time to this the age old question as to the identity of the two forms has been discussed and it is still unsettled. In this study many other branches of the broad subject of entomology have been developed. Do the two forms differ any in structure—morphologically? Certainly their geographic distribution would seem to favor the hypothesis that they are different species.

Their relations to their environment, their ecology, too, must be considered as well as their physiological reactions to the blood that may be sucked from the veins in the skin on the head or on the body.

Then comes the philosophical consideration of all of the phenomena observed—bionomics. How has the insect responded to the influences of environment? How has it adopted itself to its particular mode of life. What factors have determined the size, shape and color of the little pest and how have these factors wrought their transformations? Are the activities of this insect merely responses to chemical stimuli—tropisms—or are they due to reflexes or instinct or reason? These are the things that the students of bionomics are supposed to settle. About all that I can do in this brief paper is to emphasize, somewhat, some of the topics suggested in the last group of questions.

To live successfully means to be well adapted to the environment. An animal not well adapted must soon become so, or lose out in the struggle. Insects are the most abundant of all living creatures because they are able to adapt themselves so quickly to new conditions, or to take advantage of any changes in their environment that may be more or less favorable to them. Thus we find that species which, under natural conditions, normally fed on some wild or uncultivated plant, rapidly increasing in numbers when they have an opportunity to feed on some cultivated host plant. It is also a well known fact that a change of climate is often good for an insect's health and that they will often thrive and increase abundantly when introduced into a new environment where food is abundant and natural enemies few.

These are well known and well established facts that are generally accepted without question. But do we give these things sufficient consideration when we are studying or planning to study an insect or group of insects? Not only are the habits apt to be changed with a change of environment but pronounced structural changes may also take place and then the subject becomes of interest to the morphologist and the systematist as well as to the ecologist and the economic entomologist.

The study of variation in insects is most important and fascinating. We can not take up the study of any group of insects without having this subject soon forced into our attention. Most of us are content to merely note this, possibly to comment on it, but too few of us go deep enough to try to find out just how much variation there is, much less to try to find the underlying principles that cause and direct these variations. It is true that some very good work has been done along this line, but most of this has been statistical and has not been done by people interested in entomology. The insects have been used because they are abundant and easy to work with. The field is wide open to anyone who wishes to approach it with a wide entomological training and an analytical mind. The field is so interesting and important from many points of view that much more time and energy should be devoted to it.

Another phase of entomology that is receiving altogether too little attention is the subject of communal life, commensalism, and mutual

aid. This most fascinating field is almost wholly untrodden except for the few excursions that have been made into it by the students of ants and associated forms. Rich treasures await the explorer in this field.

We are accustomed to think of the subjects of color, pattern and mimicry as things that can be studied successfully only in some far off tropical lands. It is true that some of the most striking and bizzare examples are found in tropical or semi-tropical regions, but we have only to look about us to see most interesting examples of concealing, protective or aggressive coloration or patterns. These can be found in almost all of the orders of insects and the philosophically inclined mind will find here a wealth of material for study and experimentation. So, too, we find many striking examples of mimicry. Not long since I had occasion to try to control the larvæ of a certain sessid moth that was boring into the trunk of young poplar trees. I gave a man a small syringe and some carbon bisulphide and showed him how to use them. Returning some hours later I found that he was making very little progress with the work as the "darned wasps" kept bothering him so much. When I picked up one of the moths, which were his so-called wasps, and showed him how harmless it was, he evidently thought I was playing some kind of a trick on him and he gave up the job rather than associate with such wasp-like looking creatures. Of course we are not all agreed as to the causes of such resemblances or mimicry but the fact that the phenomona occur so often and in such widely separated orders leads most of us, at least, to believe that there is something more than mere chance or accident back of it all. We have come to look with much skepticism on the older theories in regard to the causes of these things and the efforts of American entomologists in this field have been largely critical, rather than constructive, and it is certain that a comprehensive, unbiased study of these questions, in the light of what we already know in regard to the life, structure and habits of many of our insects, would yield interesting and important results.

Another phase of the work scarcely more than touched on by entomologists is the whole field of insect behavior. Tropisms, it is true, have been studied somewhat but much yet remains to be done. When does an act pass from the realm of reflexive or instinctive behavior into the realm of habit or intelligence? Many observations have been made and recorded, but the whole question needs to be re-examined and studied in the light of what we now know about insects and better planned, more scientific experiments made to test out existing or new hypotheses.

INSECT ECOLOGY.

W. C. Allee,
University of Chicago.

Ecology is the division of biology that deals with the interrelations of organisms and their environment. We know little enough in an exact way about either organisms or their environment and still less about the interrelations. There are so many ecological problems that frequently one feels that the most important is to know where to begin and what resolutely to defer for the present.

Ecological problems fall readily into two main groups: those primarily concerned with the interrelation of the individual and his environment, and those dealing with communities of taxonomically unrelated organisms. I shall discuss the latter first.

Before going further, I should say that there are no insect communities or insect associations in nature. They exist only as an abstraction. Rarely, for that matter, are there plant or animal communities. Really there are only biotic communities, i.e., groups of plants and animals which are more or less closely integrated into a community system. Frequently on land the most abundant and important animals in such a community are the insects.

These biotic communities have long been recognized. In 1871 Verrill described them for all practical purposes among marine organisms, and S. A. Forbes in 1887 outlined very clearly some of the methods of integration in his admirable essay on *The Lake as a Microcosm.* But it was not until about 1900 that we began to have ecological surveys describing animal and plant "associations" and giving habitat lists of the taxonomically unrelated species found living near each other. Such surveys continue and are valuable in hurried, crude reconnaissance work; the vital problems in insect ecology do not consist in invading new territory and making habitat lists of the species to be found there, or even in working out the succession of different species to be found in habitats arranged in an orderly series according to physiographic age.

One group of vital problems in biotic communities is concerned with the interrelations within the community. Which species are essential? Which are accidental? Which are most important to the continued biotic balance and which are of little importance? What diurnal, seasonal, and other cyclic changes take place within the community? How nearly does the community approach stable equilibrium and what are the factors causing its stability or instability? A knowledge of such interrelationships within the community is essential for a real understanding of animal life in nature and should precede any attempt to tamper with a community by applying artificial conditions made necessary by modern economic work.

These problems can be attacked by three different methods: the statistical, that of natural history and that which may be called the method of synthetic ecology.

The statistical method lends itself to reconnaissance. It requires that collections be as nearly quantitative as possible (the margin of error being known) and that these be analyzed by applying some sort of multiple correlation formula such as the tentative ones proposed by Forbes and by Michaels. By these means one undertakes to determine statistically the closeness of the correlation existing between the species collected. Some will be shown to be accidental, others to be firmly established. Such studies have a deceiving atmosphere of finality. They are an improvement on mere habitat lists, just as those were improvements on the taxonomic check lists that preceded them, but such studies must be supplemented, for they show nothing of the reasons for the observed correlations. Incidentally, there is an excellent opportunity for anyone acquainted with modern statistical methods to develop an adequate formula for dealing with such quantitative collections.

An obvious method of supplementing and expanding the data of statistical ecology is by plain, intelligent observation. We need at the present time such field observations on the interrelations of members of insect communities by gifted observers more than we have ever needed them because now they can be of immediate importance as well as of interest. In the natural reaction from the illogical, disconnected, frequently misinterpreted but always interesting observations of many of the older students of natural history, modern ecology has neglected this important weapon of attack upon the problems of the organization existing within a given community. The method is time-consuming but may yield illuminating results without which the data from modern statistical and experimental work cannot be correctly interpreted, if indeed they can be successfully collected.

I have noticed that, too frequently, one of the major tactical problems in ecology is to persuade persons gifted with powers of field observation to check their results with adequate experiments, or even to use modern instrumentation in determining the actual conditions observed; and on the other hand to get students trained in experimental and statistical methods to do critical observation work.

Such a union of the best in the old and new methods is the aim of the modern synthetic ecologist. He desires to know all that can be known by observation, statistics, field and laboratory experimentation, and by instrumental study of the environment concerning the individual relations of the important species within the community; and from such data, he proposes bit by bit to contribute to an adequate conception of the biotic community viewed as a unit. This reverses the more usual method of the ecological survey which begins with the community and then makes such analyses as time, facilities, and inclination permit.

In order to understand the interrelations within biotic communities, we must have knowledge of the biotic conditions existing at all times of the day and all seasons of the year as well as during the daytime in the pleasantly warm months when field work is a relaxation. Remarkably little is known about winter ecology. This is an important but hitherto neglected field that rapidly repays cultivation. For example,

Dr. A. M. Holmquist has recently reported as a result of his field survey of arthropod hibernation in the Chicago area, that of 329 identified species, about nine per cent of those ordinarily solitary during the summer become more or less closely aggregated in winter. The fact of the existence of such winter aggregations has been long and well known but the extent of the phenomenon in a given population had never before been discovered, and its physiological significance is not yet analyzed. Work upon hibernation is particularly important because frequently the abundance of insects the following year is determined by their success in living through the winter. There has been equally little work upon many of the problems concerned with the sleep of insects.

Physical Relation to Environment.

Exact quantitative studies of all the factors of the physical environment conditioning biotic communities have also been neglected. Such analyses as have been made have frequently over-emphasized some easily measured factor. Thus temperature phenomena were exploited and generalizations made without knowledge, even yet imperfect, of the interrelations between temperature and humidity. But even in temperature work the improvements in technique made possible by thermo-couple developments have reopened the entire field of temperature relations. The old reproach of the natural historians that the animals themselves are more sensitive thermometers than any carried into the field by the instrumentalist, can no longer hold. An excellent example of the type of work needed along this line is furnished by the recent studies of Dr. Chapman and associates.

Recently plant and animal ecologists have been studying exhaustively distribution phenomena in reference to the hydrogen ion concentration (pH) of the soil or water to the neglect of other factors. In fact there has been a constant chase for a possible single factor index which would be a short cut to environmental analysis. In the very nature of the case, this hunt has met with the failure it deserves. The value of different environmental factors must vary in relation to other physical conditions in the environment and with different animals and at different seasons of the year.

One important physical factor that has hitherto been grossly neglected in environmental studies is that of light. For obvious reasons botanists have been more alive to the importance of this factor, particularly since the work of Garner and Allard, but the results have not been extended to insects and the quantitative measurement of illumination in natural habitats has not yet been made except in a few cases.

The recently perfected MacBeth illuminometer makes available a portable instrument applicable to hard field usage. This instrument has stood up under the hard service incident to an extended trip into a tropical rain-forest. It measures quantitatively the illumination within the visible spectrum but gives only ratios for different wave lengths. Recording instruments have also been described accurate within ± 5 per cent which make this a most promising line of investigation.

Recent laboratory developments that show the marked effects of ultra-violet radiation upon organisms indicate that we must investigate the ecological bearings of this similarly neglected factor.

Many of these environmental factors show diurnal, lunar, seasonal or other cycles. Recent studies upon the relations of lunar cycles to egg-laying of many marine organisms have established the fact that lunar periodicities are more wide-spread than was formerly suspected. This problem has not been adequately investigated among insects. The possibility of longer cycles of insect abundance corresponding to these described by Elton for mammals also deserves fresh investigation, both as to the fact of existence of cycles and particularly concerning their causation.

In this general connection Dr. V. E. Shelford has recently proposed that an endowed laboratory be established to investigate the relations between the environment and biological phenomena with particular reference to the controlling environmental factors in insect abundance, to include not only experimental work but continuous observation on the weather and the actual abundance of animals as determined by qualitative collections, etc. Sufficient progress has been made by Dr. Shelford in his studies of relations between the life history of the codling moth and physical factors in the environment to show that there are marked changes from generation to generation in the responses of these insects. He has succeeded in analyzing the causes of these variations sufficiently to bring them under approximate experimental control. Dr. Shelford finds that in the codling moth kept under identical conditions of temperature, humidity, etc., the pupal stage, for example, may vary as much as 20 per cent in length, due to preceding rainfall, temperature variation, and other similar factors. Abundance appears to be largely controlled by the rainfall of the preceding autumn and by light intensity during twilight hours.

This is a most important lead and should be followed systematically. There is good reason to believe that with competent accumulation and tabulation of data over an extended period such a laboratory could discover the fundamental underlying principles sufficiently to enable it to issue warnings of probable pest abundance; of the most profitable time for applying sprays, etc., of about the level of accuracy now found in weather predictions. Such studies should be carried out on the key members of important communities, hence the necessity for a knowledge as to which members of a community are of great importance; which as was indicated earlier, is one of the immediate objectives in community studies.

These particular studies would have more than merely economic significance for, if successful, they must be based on fundamental relations which would hold, at least in a general way, for all animals.

Another important set of problems is concerned with the relations existing between similar individuals occupying a restricted space. Such groupings are called roughly animal aggregations and their occurrence has long been a matter of record particularly in hibernation and during sexual activity. The factors that lead to the formation of such

aggregations was much discussed in the days of the tropism-trial-and-error controversy. The neglected element of this situation has been the lack of information concerning the physiological effect of such aggregations upon the aggregants.

Current belief appears to be that, aside from sexual relations and colonial insects, the crowding caused by these congregations is harmful due to one or more of the following factors: increased concentration of excrement, decreased available food per individual, increased interference, with consequent over-stimulation or grosser physical injury, and the greater ease with which the group could be caught by predators. The first three of these factors are known in many cases to cause a decreased rate of growth and a decreased rate of reproduction in insects, snails, man and other animals.

Recent work, mainly outside the insect group, indicates that the effect of such aggregations is not always harmful but that they may have real survival value for the majority of individuals due to tonus maintenance, lessening of the rate of change between the individuals and their environment and in the actual modification of their environment in a favorable direction. This last aspect is best illustrated by the fact that a given amount of a poisonous substance is frequently cleared up without ill effect by a group when the same, or even a lower concentration, is fatal for isolated individuals. Such protective relationships are not necessarily restricted to members of the same species and may very well be another one of the integrating factors in the loose organization of biotic communities. The extent of this set of phenomena needs to be established and here the aggregations known to occur at times among otherwise solitary insects appear to furnish favorable material for study. These problems are fundamental in any understanding of the organization of societies of insects, and of other animals and have an obvious economic bearing.

I have said nothing specifically of the problems of the geographic distribution of insects. In essentials the problems involved there have been outlined in the discussion concerning biotic communities. The only real difference is the geographic extent of the community investigated. It is important that such investigations be made as completely and as soon as possible in the habitats not yet dominated by man both for the sake of the knowledge of communities under natural conditions, which is valueable in itself, and for the better understanding of the preservation of the biotic balance as man's influence extends.

Finally this discussion of problems has carefully omitted the most fundamental aspect of the question. The problems outlined appear to me to be of vital importance for immediate solution but you will see on reflection that they are mainly description problems; problems in experimental and quantitative description, to be sure, but chiefly concerned with the question: exactly what is the interrelation between insects and their complete effective environment? In the prosecution of the attack on these problems much incidental light may be thrown on the fascinating and essentially more fundamental problems dealing with the mechanisms by which the environment produces the observed

effects. Frequently too, important leads will be discovered which can be followed in a systematic attack on this set of underlying phenomena. But a concerted mass attack upon the problems of the mechanics of the interaction between animals and their environment will be seriously hampered if we do not have a greater accumulation of knowledge than at the present time, concerning the extent and the character of the effects to be explained. Incidentally the immediate problem is infinitely the easier of the two.

LITERATURE CITED.

Allee, W. C. 1927. Animal Aggregations. Quarterly Review of Biology. (II, 368-398).

1926. Distribution of animals in a tropical rain-forest with relation to environmental factors. Ecol. VII, 445-468.

1926a. Measurement of environmental factors in the tropical rain-forest of Panama. Ecol. VII, 273-302.

Chapman, Royal N., and Associates. 1926. Studies in the ecology of sand dune insects. Ecol. VII, 416-426.

Elton, C. S. 1925. Periodic fluctuations in number of animals: causes and effects. Br. Jour. Exp. Biol. II, 119-162.

Forbes, S. A. 1887. On the local distribution of certain Illinois fishes. An essay in statistical ecology. Bull. Ill. State Lab. Nat. Hist., VII, 273-303.

1887. The lake as a microcosm. Bull. Peoria Sci. Ass., 1887.

Garner, W. W. and **Allard, H. A.** 1920. Further studies in photoperiodism; the response of the plant to relative length of day and night. Agri. Rev. XXIII, 871-94.

Holmquist, A. M. 1926. Studies in Arthropod hibernation. I. Ecological survey of hibernating species from forest environments of the Chicago region. Ann. Ent. Soc. XIX, 395-428.

Kimball, H. H. 1924. Records of total solar illumination and their relation to daylight intensity. Mon. Weather Rev. 52:475-79.

Legendre, R. 1925. La lune et les etres marins. Revue Scientifique. Paris. 63d annee, Apr., 1925, 225-236.

Michael, E. L. 1920. Marine Ecology and the coefficient of association; A plea in behalf of quantitative biology. J. of Ecol., VIII, 54-59.

Shelford, V. E. 1926. Methods for the experimental study of the relations of insects to weather. Jour. Ec. Ent., XIX, 251-260.

1927. The Codling Moth. Bull. Illinois Nat. Hist. Survey, (in press).

Verrill, A. E. and **Smith, S. I.** 1871. Report upon the invertebrate animals of Vineyard Sound and adjacent waters. Report U. S. Fish Comm., 1871-72 (1874) 295-778.

NEEDS IN THE STUDY OF BENEFICIAL INSECTS.

L. O. Howard.

I take it for granted that, in wording this title, the committee had in mind only those insects that are beneficial by preying upon injurious species, and not the honored honey bee or the domestic silkworm or any of the dozen other forms that in one way or another are or have been useful in the arts and industries. Nor do I take it had the committee in mind the insects from which we derive ethical benefits—and indeed these benefits are doubtful. The sluggard will never go to the ant, no matter how many times he has been told to do so since the Holy Bible first took form. Rather, does the ant go for the sluggard!

Naturally our great need in the study of beneficial insects is to gain knowledge that will help us to foster them to the best advantage. If we could domesticate them and use them at will it would be ideal. Possibly with some species a condition approaching this may be brought about. Indeed, it has been brought about in California with *Cryptolaemus montrouzieri*. There, as you know, a stock of Dactylopius is kept up by feeding them on potato sprouts kept in great sheds in such number that an almost unlimited supply of Cryptolaemus is readily furnished to the citrus growers in a more or less commercial way.

Possibly the same situation may be brought about with other enemies of injurious insects, but it is unlikely. We cannot speak positively until we have tried out all the possibilities, and it is in the study of these possibilities that we will find our greatest gaps of knowledge and hence our greatest needs. Just as in the study of injurious insects, it comes right down to the plain statement that we must know everything about them.

First we must have names for them all, and a stable nomenclature. Hence the need for more skilled taxonomists in the parasitic Hymenoptera, in the parasitic Diptera and in the predatory groups of the Coleoptera and Heteroptera.

Second, we must know intimately the biology and ecology of all of the enemies of the principal injurious insects of the whole world, and, after that, of the species of secondary importance.

This should be taken up, of course, species by species; and group generalizations will soon be possible. Some fairly accurate generalizations can be made already, from a study of recorded host relations, but there have been only a few careful studies of the exact life histories of individual species, studies which include details of behavior as well as of the vital processes that must be understood.

The species taken up consecutively will most readily be the parasites or predators of some special host. Little is usually done except to record them by name (and even this is too often incompletely or faultily done). Suppose that such natural enemies of a given host of importance have been studied with care and their biological peculiarities well worked

out. Then, after a series of such comprehensive studies, we will have a sound basis on which to begin generalizations as to group biology.

In America we need very greatly workers who are able and willing to go at this biological task. Men and women of any degree of training can help—can do work that will tell. Every careful observation counts, ***provided it is recorded in print.*** The publication of short notes on individual observations in this direction is greatly to be desired. No one, for example, appreciated the biological importance or rather general occurrence of the feeding of parasitic Hymenoptera at the puncture hole in the host made by the parasite's ovipositor, on reading Paul Marchal's first note of an isolated observation in 1905. ***But he recorded it,*** and other observers read his note, and year after year in different parts of the world corresponding observations were made with other species, and the habit now assumes an economic interest and a very pronounced importance to the student of evolution.

We need as many men as possible in every part of the world to study the biology of beneficial insects. In America, so far as I know, there are no independent workers at the present time engaged in such investigations; and in the laboratories at Melrose Highlands, at Arlington, at Riverton, New Jersey, at Monroe, Michigan, and at Chatham, Ontario, where the parasites of the gipsy moth and brown-tail moth, of the European corn borer and the Japanese beetle are being intensively studied in the effort to establish them in this country, there seems to be a disposition to withhold publication until many things can be recorded at once.

In France there seems to be a better disposition toward prompt publication, and interesting articles are appearing from time to time from a group of observers including Picard, Lichtenstein, Faure, Trouvelot and Voukassovitch. This should be done in this country. It is a disappointment that the early very important and significant notes published especially by Timberlake and Harry Smith about some of the aspects of their work in the parasite laboratory at Melrose Highlands were not followed up by a rapid series of similar publications from that laboratory. It seems a pity that Harry Smith has not been able to get back to work of this character. It seems a pity that Timberlake has devoted the most of this time in recent years to taxonomic work rather than biologic work for which he is so admirably fitted.

America has at the present time only one institution where work of this kind is being carried on, and that institution, curiously enough, is in France. Thompson and Parker at Hyeres are independently making studies of great interest, and, inspired by Doctor Thompson, a young Frenchman employed in the laboratory, P. Genieys, wrote up some observations which I considered of importance enough to translate into English and which the Annals of the Entomological Society of America thought worth while to publish in their journal.

Doctor Thompson has a philosophical mind and broad training in biology; and it is a pleasure to know that another young American entomologist, also broad-minded and admirably trained, is using part of his time allotted on his fellowship for foreign travel in visiting Thomp-

son at Hyeres and in discussing these questions with him at length. I refer to R. N. Chapman.

We can imagine Doctor Thompson and Doctor Chapman, possibly at the present moment, sitting in the laboratory over there, discussing ardently the broad aspects of natural control, and in all probability discussing this very question—the needs in the study of beneficial insects—and with equal probability bringing out many points which will escape your present speaker. But it goes without saying that they will not argue the point we have just discussed, namely the need of infinitely more work on the intimate biology of parasitic and predatory species. That is self-evident and is basic in any plans for their utilization.

The main trend of practical work with these forms for the past forty years has been their use against imported insect pests. This work has been not only practical, but it has been spectacular and in several instances absolutely dramatic. It has appealed to everybody and has helped to arouse the necessary popular interest in the work of the economic entomologist. Its possibilities have perhaps been exaggerated. Surely it has aroused false hopes as to its ease of accomplishment. I mentioned this in my address at Kansas City last winter in more detail than is necessary at the present time.

Much of this international work is now going on. It is bound to continue. Much time and money has been wasted in the past. Probably much (though not so much) is being wasted now year by year. But this waste is being lessened, and will continue to be lessened more rapidly as we learn more and more about developmental details of individual species and of groups of species. The gaining of such knowledge will not only gradually (very gradually) reduce the necessary amount of foreign travel by experts, but it will bring together a mass of facts that will prevent waste of time in experiment concerning the proper periods and best methods of shipment of parasites from foreign ports and in the best methods of caring for them, rearing them, and liberating them in the regions to which they are sent.

All of this presupposes a very general knowledge by all of the workers about what is going on elsewhere. Again the necessity for the publication of short notes is evident. More than this, no opportunity should be lost which will bring the workers together. To read accounts of how Harry Smith and his fellow workers do certain things in southern California, and of how similar things are done by Smith, King and Allen at Riverton, Jones at Arlington, Atwell and Stearns at Portland; Muir, Fullaway, Swezey and F. X. Williams at Honolulu; Clausen, Gardner and Jaynes in the Orient; Marchal, Vayssiere and Trouvelot at Paris, Thompson and Parker at Hyeres, Berlese and Del Guercio at Florence, Silvestri at Portici, or Webber in Hungary, is all very well; but if they could visit one another from time to time, study individual methods and talk them over, progress would undoubtedly be more rapid.

In this list I have not mentioned the workers at Melrose Highlands nor Babcock's travels in Europe in his study of the ecology of the European corn borer in its native home; but Webber and Muesebeck of

Burgess' laboratory are supposed to return to America from time to time, as has been the case with all of the parasitologists of that laboratory; and at Melrose Highlands they are close enough to Arlington so that the methods in both laboratories are undoubtedly well known to the workers in both.

Caffrey goes from Arlington to Monroe, Michigan and to Chatham, Ontario, from time to time and carries news from Jones to Luginbill and Baird; Silvestri is a world traveler, and Trouvelot is probably coming to America next spring. The problem of L. B. Smith and his associates King and Allen with the natural enemies of the Japanese beetle is rather different in its character. But Harry Smith and Timberlake should at least visit eastern laboratories, and our eastern workers should go out there. Thompson should come to America for a comprehensive trip for his own information and for the good of all of us. And so on, and so on.

A broad statement as to international work which I have made before* may well be repeated here. Since there exist all over the world beneficial insects, many of which can be acclimatized here and some of which undoubtedly will prove of value to American agriculture, carefully planned work should be begun looking towards the increase of our insect population by the addition of as many of these beneficial forms as possible. Results of striking value perhaps could not be expected speedily, but it seems clear that this work should be done. And it will be well for every other country to do the same thing.

Peculiarly open as we have been in this country (and still are to some extent, in spite of the beneficent work of the Federal Horticultural Board) to the introduction, rapid development and spread of foreign insect pests, we have neglected too long the possibilities of native parasites and predators, and I propose the consideration of such possibilities as one of our needs. Not only should we make careful studies of our native species, so as to be in position to help foreign governments which may be threatened with damage by American pests (and this is especially liable to occur to any of the nations lying to the west of the United States), but in our wide-ranging country there are doubtless instances where we can use our own species.

It is surprising how little scientific attention has been given to such possibilities. One's mind goes at once to the large-scale collection of adult Coccinellidæ in the California mountains for distribution among the melon growers of the lowlands, but we have had no scientific analysis of the results of this work although the insects were collected and liberated literally by millions. The work was popular with the growers, and it doubtless brought funds and popular applause to the State Commissioner of Horticulture, but we are in the dark as to the extent to which the results were beneficial or indeed as to whether the work helped at all.

Nevertheless this elaboration on a truly Californian scale of the old European gardener's custom of placing a few ladybirds on a plant badly

*Year Book, U. S. Dept. of Agr., 1916, p. 288.

infested with aphids should be studied scientifically. Plant-lice multiply so rapidly that if we can give their natural enemies an abnormally early or an abnormal numerical start there may be some gain—some advance of the date at which every year the native enemies control the pests.

Of course we must look at things differently when we are working with insects of a different group; expecially when they belong to a different order. Therefore, as bearing upon the question we have just raised, it may not be fair to draw positive deductions from the most interesting experimental work carried on by Webster for the Bureau of Entomology in 1907. This experiment was with the Aphidiine parasites of *Toxoptera graminum*, the so-called green-bug of Texas. Webster, it will be rembered, took two widely separated four-acre fields of winter oats near Manhattan, Kansas. One of these fields was used as a check. Into the other were introduced some millions of parasites sent from Wellington, a point much further south. Careful counts were made from time to time, with the result that the percentage of parasitism in the field into which the millions of parasites had been introduced did not increase quite as rapidly as it did in the check field. It should be mentioned that a somewhat similar experiment was carried on about the same time by S. J. Hunter, who thought that he had good results. Incidentally it may be mentioned that Hunter's claims caused the writer some embarrassment in his hearing before a congressional committee the following winter.

On the other hand, we have another experiment of Webster's with native parasites, carried out the same year (1907). At Lansing, Michigan, and Marion, Pennsylvania, a bad Hessian fly infestation occurred. Examination showed that ninety per cent of the puparia had been parasitized by a species of Polygnotus. A field of wheat near Sharpsburg, Maryland, was infested by the Hessian fly at the same time, and careful examination showed that no parasites were present. On April 8th a large number of parasitized puparia were brought from Marion, Pa., to Sharpsburg and placed in the field. On July 8th the percentage of parasitism was almost one hundred. The writer detailed these two experiments in his address before the Seventh International Zoological Congress at Boston in August, 1907, on "The Recent Progress and Present Conditions of Economic Entomology," and stated "This is the most striking example of the kind that has yet been recorded, and indicates the value of further experimental work in this direction."

It should be stated that later attempts were made to establish this same parasite of the Hessian fly in California, but that they failed.

Occasional experiments of this general nature have been made since, but undoubtedly many opportunities for informative experimentation have been lost. Carriage of parasites for great distances in order to make a good test is not always necessary. Van Dine, for example, down in Cuba, is finding that the Tachinid parasites of the sugar cane borer at times seem localized. Another example of extreme localization was noticed in the city of Washington in 1896 and 1897. Tussock moth caterpillars were very generally defoliating shade trees. In

certain sections of the city, however, parasitism by several species reached a very high percentage, whereas less than a mile away it was not evident. In this case the parasites probably would have spread slowly, but the possibility of an easy hastening of the spread by artificial carriage was plainly indicated. Such experimental opportunities as this must not be neglected.

Thus far in this brief paper I have been discursive, perhaps to an extreme, but to those who have followed me must have come the underlying thought that I have realized all along that most of the practical work that has been undertaken with parasites has been of a more or less haphazard character—that we have not known enough of the general principles that govern what we entomologists call parasitic relations, and that an enormous number of specific studies and observations must be made before we can attempt to formulate such general principles.

We cannot predict the success or non-success of any given species carried into a new environment even though one of its preferred hosts occurs there in enormous numbers. We do not know the seasonal history of most of those forms that have multiple hosts. We do not know why a species is abundant in one year and rare the next, except for the occurrence of hyperparasitism or for the fluctuation in numbers of its host or hosts, due possibly to the parasite's own work. In fact, a vast field for workers is open.

Therefore let us encourage as many men as possible to take up the study of parasitic and predatory forms, and let us resolve to let no opportunity pass, however trivial it may seem, to make and to record observations which may help to shed light upon any phase of these strange and important lives.

Then will come the architect who will see that all of the bricks and timbers acquired by these individual workers will be brought together in a harmonious structure satisfactory to the critical mind and of great practical value.

Added note.—Since this paper was written it appears from current publications that several workers in America have realized the situation as I have outlined it and have been doing just the work that I have pointed out as desirable. I may mention especially the recent papers of Dr. Grace H. Griswold of Cornell, the very interesting study of the parasites of Syrphus flies by Dr. M. Kamal, carried on under Harry Smith at Riverside, and perhaps especially the remarkable papers published in current numbers of the Annals of the Entomological Socirty of America and the Journal of Economic Entomology by Dr. W. V. Balduf of the University of Illinois.

ECONOMIC ENTOMOLOGY.

The Needs in the Study of Insect Injuries.

E. O. Essig,
University of California

The scope of this paper is construed to mean the needs of further study in the field of the actual injuries or losses occasioned by insects and may rightly embrace either animal or plant life. However, the nature of this symposium is such that it is thought best to include only references to plant life and more particularly to crops of commercial importance.

Diagnosis of insect injuries is one of the first principles of economic entomology. To do this correctly and quickly requires a thorough fundamental training and a long rigorous experience: a fundamental training to be able to recognize the insect and its work and experience to sum up the real or estimated amount of injury done or likely to be done, and to prescribe the proper remedy. A deficiency in any one of these may result in great losses, due either to lack of or to misdirected recommendations.

I think that it is not necessary for me to enlarge upon the needs of training and experience as requirements for the recognition of insect pests in all their stages, and the types of injuries caused by each, except to point out that more than scholastic attainments are necessary. I have in mind a case of a caterpillar infesting several thousands of acres of a certain crop which was just getting established in a new district. A large amount of capital was involved, certain huge contracts for planting were ready to be signed, equipment was being prepared on a big scale. This unforseen infestation was like a thunderbolt—everything connected with the venture was paralyzed. The farmers and promoters were thoroughly frightened. These questions were raised: What is it? Is it a new pest? Will it destroy all of the crop? Will it appear every year? Can it be economically controlled? Everyone in the neighborhood gave it the "once over," but no one had ever seen or heard of it before. Then experts were called to the number of at least a dozen from all available sources and with many kinds of experiences. They looked it over. Many views were expressed to the farmers and promoters, but they were for the most part contradictory and unsatisfactory and did not answer the most important questions. In other words they were guesses. However, one finally arrived, who was familiar, not only with this crop, but the other crops of the state. He knew the caterpillar, had known of its presence in the state for ten years, had seen it on many other crops and on the very same crop in the exact neighborhood in small numbers the year before. He had previously reared adults and had them determined at the National Museum and had preserved mounted specimens not only of all stages of the insect, but also examples of the work. This evidence was convincing. The interested parties were informed that the attacks would

be spasmodic and infrequent, that they were never ruinous, that the caterpillars could at once be combated at a small cost and the work was begun immediately. Three days had been lost in useless consulation, but in three days more the situation was completely cleared and perfect confidence was restored.

In considering insect injuries and the amount of damage occasioned by them, it is the usual practice to compare the final harvest of an infested crop with that of an idealistic normal crop where no insects are present, without taking into account any of the many factors which may have influenced crop production for that particular year. I know that this is the case because all of the estimates of insect damage are based upon a certain percentage of normal production. These figures are of great value in impressing the uninitiated and in securing needed appropriations, but they mean little in actual farm experience. As an example take the cotton boll weevil. The yearly estimated losses due to the ravages of this insect would support the government and should at least cause a cotton grower to pause before planting another crop, and yet we find that during the past year so much cotton was produced that it became a drug on the market; that in order to control this insect, cultural methods have been adopted which results in a far greater production of cotton under weevil conditions than where weevil does not exist; that on the whole the weevil has been a blessing to the cotton industry. Similar statements have been made concerning the alfalfa weevil in some parts of the Great Basin. I am not vouching for the authenticity of any of these statements, but they indicate that we have not succeeded in presenting the facts; that a different basis for estimating insect injuries is needed.

As I look at economic entomology in relation to crop production it appears to me that the only thing that counts in actual field practice is the ***amount of the infested crop saved above the cost of control.*** If this does not exceed the cost of control it is not warranted and becomes a useless waste of money and energy. An apparent exception, however, which bears on the problem, is a case where the cost of control measures may not be warranted by the amount saved that year, but may be thoroughly justified by preventing a reoccurance of the pest the following year. It is therefore necessary for the economic entomologist to be familiar with crop production and farm practices in order to make a proper estimate of such injuries. For instance an estimate of injury due to the codling moth made before thinning, might be greatly under or over estimated if the entomologist did not take into consideration, not only the actual process of thinning, but also the disposal of the infested apples removed from the trees. The value of the crop is also often entirely overlooked. I recall recommendations made to control the larvæ of the pasture crane fly, amounting to only $3.00 per acre, which seemed small enough, but was out of the question when the pasture was only worth $2.50 per acre. Such cases may be enumerated at length.

Many ingenious methods have been suggested as a means of securing uniformity in estimating injuries and losses occasioned by insects, but

these usually fall short of practical application because of the many uncontrollable factors with which we have to deal. Laboratory tests and field tests on a small scale are valuable in determining essential points, but they cannot be relied upon until fully tested and found satisfactory under practical field conditions.

In determining the amount of injury as a basis of recommendations for pest control it is necessary to know how much loss of foliage or fruit is permissible without actually interferring with the production of a satisfactory crop. Thus it may often be a distinct advantage to destroy a certain percentage of both fruit and foilage and in other cases, while such destruction may not be desirable, yet the actual damage to the tree may be so negligible as not to warrant control. In contrast to this type of injury the crop may be so severely injured that the cost of control measures would only be adding to the misfortune, except as already pointed out where a reoccurring pest may be eliminated for the next year. Between these two extremes, that is somewhere from a minimum of 15% or 20% to a maximum of 70% or 75% injury, control is usually always warranted and it is the ability to recognize this point that is most needed.

One of the outstanding needs in economic entomology is a study of the injuries caused by fungous and bacterial organisms carried by insects. Because this field lies within the domain of entomology and plant pathology it has been neglected by both. However, since the discovery that certain mosaics, potato tip burn, curly top of sugar beets and other diseases are transmitted by insects this field is attracting many workers so that some of the obscure injuries to plants which have puzzled entomologists are becoming known. One thing is sure: unless we know what is causing the injury we cannot intelligently prescribe the remedy.

In closing I may say that I do not believe that uniform rules can ever be formulated to cover the needs so imperfectly discussed in this paper. Training, skill, judgment and experience are not reduciable to formulæ but they can all be cultivated and increased.

In summing up I should like to emphasize the following points:

1. The need of wide training on the part of the economic entomologist, particularly in agricultural botany, so that he may better understand, not only the types of injuries, but the lasting effect of the same on the individual host plants and on a crop.
2. The need of detailed studies or observations of the feeding habits of the various stages of insects in order to be able to properly diagnose the case at hand.
3. The need of the constant varification of data to reach practical conclusions.
4. The need of a careful study of the complete situation before reports or recommendations are made. The need of sane conservatism in estimating losses due to insects—these losses are sufficiently great to require no exaggerations.
5. The need of recognizing the importance of conserving the farmers income by not recommending measures unless they are fully

warranted as well as to emphatically urge control when by such means the crop may be saved from insect depredations.

6. The need for further studies by entomologists, plant pathologists plant physiologists, and bacteriologists to broaden our exact knowledge as to *how* insects *injure* plants.

7. The study of the past history of insect pests to properly estimate the probable results of present attacks.

NEEDS IN THE STUDY OF CONTROL MEASURES.

W. P. Flint.

It often seems that we have advanced only far enough in our work of insect control so we begin to realize how ignorant we are. There is certainly need for further studies in practically all lines of insect control. It is obviously impossible to say what studies are most needed at this time. The control which is satisfactory today may be of little value in a few years, owing to changing conditions, or possibly to adaptations of the insect which has rendered it more difficult to kill. At the last Pittsburgh meeting of the Association of Economic Entomologists, Professor O'Kane presented a review of control measures, rating the methods according to their efficiency in combating different species of insects. The standing of the control measures for the insects listed being based on the replies received to a questionnaire sent out to a large number of entomologists. It is quite certain that if the same paper was presented today and the ratings of control based on the opinions of the same entomologists, that the degree of effectiveness given for the control measures would vary considerably from that given in 1918, and that the rating of control for certain insects would not be as high as it was eight years ago. This shows that in all our work on insect control, it is necessary to constantly study the results being obtained by control measures which have been considered satisfactory. Such studies are necessary to be sure that an unfortunate situation does not develop where the measures being advocated have ceased to be as effective as formerly, and the insect pest which we are trying to control be permitted to increase to a point where heavy damage may occur. A very good example of just such a condition is afforded in the increase in San Jose scale in the central states during the years of 1918 to 1922. In other words, it is not sufficient that we work out the facts concerning the life history and habits of an insect and develop an effective control, but we must continue to study the insect and the results of the control.

Further studies are badly needed in what we may term, insect behavior, after the life history of an insect has been worked out for a

certain region with a reasonable degree of exactness. We are badly in need of further and more intensive studies on the behavior of the insect, or as we may style them, detailed ecological studies of the response of the insect to all factors of its environment, in that region and for as many different localities as possible where it is destructive, and where it occurs, but does not cause damage. Dr. C. H. Townsend in a recent paper in Ecology,* has outlined very clearly some of the work needed along this line. Such studies are necessary for all of the more commonly injurious species of insects. We can not hope to reach the highest degree of efficiency in insect control until we have a more definite knowledge of the exact effect on the insect, and the control measures of such factors as heat, sunlight, rainfall, wind movement, humidity, abundance or lack of favorite food, and many others. It is necessary that we should plan such studies to extend over a period of years, as immediate results of any value can not be expected. In most cases, the entomologist has felt that pressure for immediate results was such that it was not possible for him to carry such studies over any very long period of time, and in many cases, the demand for immediate means of control for a number of different insects is impressed so strongly upon the entomological workers that while the need of a long time program is recognized, it has been impossible to carry it out. Perhaps we can gain something from studying the methods used by the agronomists, where their experiments are often laid out with no idea of definite results for ten or more years.

Hibernation.

Another line along which control studies are badly needed is that of the actual effect of crop rotation on insects. A brief review of the recommendations given in several of the leading books on economic entomology shows that crop rotation is recommended as a control measure for approximately 60% of our destructive forage and field crop insects. How much actual data can be presented showing definitely the effect of crop rotation on increasing or decreasing the number of insects in a given field, or a given agricultural area. A rotation that will place a legume crop in fields heavily infested with an insect that feeds exclusively on grasses, is certainly of value, but how much information do we have on what actually occurs in such fields and as to the exact effect of a good system of rotation, or one that is generally recommended by entomologists on the insect population of a field, a farm, or a locality where such a rotation is generally followed. Studies along this line are difficult to make, and to be of any value, must be carried through a long period. They are certainly badly needed. Much the same may be said regarding the need of studies of the effect of cultural practices on insects. That certain cultural practices will have an effect in reducing the numbers of insects in the field we know, and we have some definite information on the actual effect of different practices on insect populations. No one familiar with the facts in the case, and the

* Ecology Vol. 2, page 326–337.

meager amount of data which we have to present to back up our recommendations would say that there is not a very decided need for further study along this line, and the accumulation of much more definite information than is now available on the effect of cultural practices on insects under the varying conditions which may occur in the same region during different seasons.

Agronomy Relations.

Another line of needed study which is now being taken up, is on the tropisms of insects, of these, studies of the Chemotropisms are of special importance. We have been going on year after year applying sprays for insects that are leaf feeders, and have paid but very little attention, as to whether or not these applications were repellent, or attractive to the insects which we were trying to control, at least so long as they were not so strongly repellent as to actually prevent feeding. The relatively small amount of work that has been done in actually testing the response of insects to different chemical stimuli, producing different odors and flavors, has shown that there is an ample field for intensive studies along this line, and that it is reasonable to suppose that we can greatly improve the efficiency of many of our poison sprays if they are prepared in such a way as to make them really attractive to the insects we are trying to combat. Perhaps the best example of what may be done along this line, is the recent work carried out at the Japanese Beetle Laboratory, where it has been found possible to actually attract the beetles for a considerable distance to certain shrubs or trees that have been sprayed with a chemical giving off an odor attractive to them, and then destroy them by the use of a contact insecticide. Studies along this same line may make it possible for us to give our main attention in the future to spraying only certain rows of trees in our orchards and gain a better protection from some of the orchard insects than is the case with the methods we are following at the present.

These are only a few of the many lines along which further study in insect control is greatly needed, and some of the things which must be done if we are really to keep our science abreast of the developments in other lines. For the past ten or more years, insects as a whole, have probably been gaining rather than losing in their fight with man. This fact, if we admit that it is true, brings out sharply the need for further studies on insect control.

SUMMARY.

E. F. PHILLIPS.

It pays occasionly to take stock to see what has been accomplished. In the present discussion we have gone beyond this by outlining the work needed for a more effective attack on the unknown. Naturally each speaker has emphasized the needs in his own field, yet each one has had it in mind that every other aspect of Entomology is equally in need of further work if the Science is to progress along proper lines. Each of us can readily think of many more needed investigations. It is impossible to summarize this discussion, in a narrow sense of the word, and all that one can do is to attempt to outline the general needs in the light of what has been said, while running the risk of becoming philosophical or of expressing platitudes.

Every one must be impressed with the need of more and better work and of more and better workers. A member of this Society recently compared present progress in Entomology with that of an attempt to tunnel the continental divide with teaspoons, and while the situation is perhaps better than his simile would suggest, there are so many things that we wish to know that somtimes progress seems rather slow. Each newly discovered fact increases the number of things which we wish to know. Instead of feeling hopeless, we should recognize it as a duty and privilege whenever and wherever possible to encourage the teaching of Entomology, in the hope that among those thus taught there may be some who have that peculiar type of mind needed to help extend the boundaries of our knowledge in some of the needed directions.

Future investigations in Entomology will include more than a study of insects. Statistical methods, Chemistry, Physics and other scientific facts and methods must be used to enable us to cover the field even now presented. I was especially impressed by Doctor Kennedy's suggestion to apply zonal studies to control measures in Economic Entomology. If I may refer for comparison to a field not previously discussed, in Apiculture we have for some time been studying the relation of soils to the suitability of a region for commercial beekeeping. When some years ago I asked the Federal Bureau of Soils for information, I was told that I was one of the very few workers in other fields who was attempting to utilize soil surveys. Vegetation types often follow soil types, and in many instances the physiological condition of plants is clearly influenced by soil composition and physical character, so that we can not afford to neglect such lines of biological investigation.

A most vital problem, after all, is the proper teaching of Entomology. In presenting the subject to those who will be the investigators of the future, the teaching can no longer be confined to entomological studies proper, if we expect them to become the type of workers which is demanded. This can be brought out best by reviewing the evolution of Entomology. The first step was obviously the descriptive one, Taxonomy, and at first this consisted largely of collecting and classifying

adult insects, not the future type of Taxonomy which has today been presented. Next came the second descriptive stage, Morphology, but again not the future type. During the descriptive stage of biological science there developed the great philosophical concept, Evolution. Gradually insects came to be looked upon more as living units in a community of life rather than dead adult specimens to be pinned or dissected, and this brought in Physiology, Ecology, Parasitology, Embryology and other lines of investigation which deal with behavior, life processes and inter-relationships. These later studies make it necessary that the student call to his service Chemistry, Physics, Meteorology and more recently allied lines of biological investigation aside from Entomology itself, such as plant distribution, morphology and physiology, soils as a living entity, comparative psychology and the like. In short, progress has been brought about by widening the field of Entomology to include almost the whole gamut of sciences, while at the same time we have narrowed it by each selecting a small corner in which to work. It is interesting in passing to note that the philosophic phases of the subject attract less and less attention as the horizon widens, since finally all must realize the futility of attempting to grasp the meaning of the whole. Detailed behavior studies indicate that insect species vary greatly in their adaptability to new environmental conditions. Most of them appear to have little adaptability because of instinctive limitations or because of morphological specialization and consequent specialization in physiological function. We dare not make analogies between even closely related species but must conduct investigations in behavior and physiology for each species. This outline of the evolution of Entomology indicates the need of broad training for the future entomologists, if they are to conduct the investigations which have previously been outlined.

The pressure for results along economic lines has often resulted in enlisting in the work, men who do not have adequate training to undertake investigational work. In many cases it is necessary that control measures be advised before there is time to undertake investigations along physiological, ecological and other biological lines. One can not in the least blame the public for demanding remedies, nor can one justly blame the entomologist for giving out the best possible advice, yet it is extremely unfortunate if the advice bears unwarranted earmarks of finality. The advice may at times contribute to results almost as bad as the damage of the pest itself, unless every phase of the subject is given full consideration, as witness the difficulty this year in the Northwest with arsenical residues.

Today it is not possible for any one entomologist thoroughly to know more than a small part of the field, and this is becoming more and more true each year. This indicates that workers of the future must be still more highly trained and highly specialized, but this brings up a serious problem. The person who too soon specializes to to high a degree misses a considerable part of the fun of his work, for his outlook is too rapidly narrowed, so that at no time can he stand upon the mountain top and view the whole field, even though through a haze.

The old workers in Evolution made much of the dictum that Ontogeny recapitulates Phylogeny, and it may be that the best training for the young and enthusiastic entomologist is to lead him through much the same stages through which the Science has passed in its evolution, thus giving him for a while the pleasure of the philosophic aspects of the subject. In other words, it may not be wise to lead him too early into specialization, but rather to allow him for a time to enjoy himself by being in a sense an old time naturalist and philosopher. If he begins early enough, this entails no serious loss of time. Progressively, but of necessity rather rapidly, he can be led into a narrower field, yet at the same time a broadening one, by giving him the fundamentals of those parts of Chemistry, Physics and other branches of Biology itself on which he must depend. The serious danger here, from the standpoint of the teacher, is in knowing into what allied lines of work each student should be led, for he can not enter them all. There is danger that each teacher will emphasize too greatly the requirements of his own limited field and that the beginning student may not have a free opportunity to choose for himself. Naturally no one institution can offer all the work which even now has a bearing on entomological investigation, and this will doubtless lead still more to specialization between the institutions themselves, which may be a bit rough on the students, unless in some way they may be able to go from one institution to another freely. The broad training needed for the future will not only create interest on the part of the student but will indicate to him that Entomology is something more than the squirting or dusting of arsenicals on the tails of insects. In fact this is scarcely Entomology at all, any more than horse-shoeing is animal husbandry. Applied courses given too early in the training and experience of the student should and do give him a biased view of the Science and are apt to repel him from further work.

There are fads and fashions in science as in clothes, and whenever a new means of investigation comes to light, there is danger that the value of a single factor may be over-estimated. This Doctor Allee has pointed out with mention of the recent work on hydrogen-ion concentration. In the whole field of Zoology, one can not fail to recognize the waves of subjects and methods which have passed, and lines of work formerly much stressed are now quite obsolete. Day before yesterday it was statistical method, yesterday it was hydrogen-ion concentration, today it is something else and tomorrow the style will again change. There is much to be said for the worker who reads and uses the results of such fashionable work but who steadfastly refuses to be carried away.

When we are confronted by a situation such as this, there almost invariably arises some supreme egotist who thinks that he is better able than anyong else to organize the work of the future and who advocates a strict coordination of the work along those lines which appeal especially to him. The investigator is an individualist and must be allowed to go his own gait, except for such wise guidance as may be available. In only a limited way is detailed direction tolerable, and this occurs when the public, through its legislative bodies, determines that a

certain line of work is needed for the benefit of the public itself. In that event, the executive charged with the conduct of the work must see that those employed for the work shall confine their attention largely to the work outlined in the appropriation, but even in such cases a considerable degree of freedom has given the best results. For some years I worked under the direction of the man whose administration has largely made Economic Entomology what it today is. Many think that they know better than the Chief how the Bureau of Entomology should be administered and some designate as administrative weakness the freedom which Doctor Howard allows. Those who know agree that this so-called weakness is the one thing which has done most to make his administration effective.

An even more wholesome method of coordinating work is that observed when a leader in Entomology, such as a competent teacher, gathers about him a group of cooperating workers, all interested in related subjects but each with his own small problem. In this case the cooperation is voluntary, done because of an interest in the subject and under the direction of a leader who has a broad view of the meaning of the individual investigations and of the selected field as a whole. In this case there is not even that administrative pressure necessary in economic investigations, and the success of a strong leader is proof of the desirability of just as little administration and organization as possible. We hear much of the benefits of cooperation, in scientific work as elsewhere, but it is one of the oddities of the race that we cooperate only when there is no other course available or when it is proven that each of us will receive personal and tangible benefits. This calls for wise leadership, not dictatorial methods.

In short, the previous papers indicate that Entomology needs something comparable to an old fashioned revival of religion, without, however, any misrepresentation of values or of the opportunities for future employment, not Rotarianism but the creation or revival of interest in students. For leadership in this work, we need men of broad vision, capable of seeing the relationships between the many lines of work already conducted, capable of planning new fields for investigation and with courage to enter these fields, and also capable of coordinating investigations and of enlisting voluntary cooperation, but Entomology has not come to such a pass that it needs a Mussolini to direct it. Let us hope that entomological work may always be conducted along democratic lines of free and unrestricted cooperation. As Doctor Allee has said regarding Ecology, it is hard to know where to begin and what to defer resolutely for the present, but this decision and others must be left largely to the judgment of the individual and to the voluntary following of wise leadership. After all, leadership is the greatest need in Entomology, if I interpret the previous papers properly, and with wise and constructive leadership the needed investigations which have been pointed out by former speakers will follow as a matter of course.

THE BIONOMICS OF ANASTATUS ALBITARSIS ASHM., PARASITIC IN THE EGGS OF DICTYOPLOCA JAPONICA MOORE (HYMEN.).

By CURTIS P. CLAUSEN,

Entomologist, Bureau of Entomology, United States Department of Agriculture, Shillong, Assam, India.

INTRODUCTORY.

During the late winter months of 1920 the writer observed numerous large, conspicuous egg-masses of the Saturniid moth *Dictyoploca* (*Caligula*) *japonica* Moore upon the trunks and larger branches of various deciduous forest trees in the vicinity of Yokohama and Tokyo, Japan, and further observations showed it to be a pest of *Prunus* spp. as well as chestnut and camphor. A number of these egg-clusters were collected at the time and set aside for parasite rearings, with the result that a considerable number of a Eupelmid, later determined by Mr. A. B. Gahan of the U. S. Bureau of Entomology as *Anastatus albitarsis* Ashm., emerged, accompanied by a smaller number of an undetermined Trichogrammid.

In the following season it was noted that the larvæ of this moth were inflicting extensive injury to deciduous forest and shade trees, at times amounting to complete defoliation, and this condition persisted during the five years the species was under observation. The life cycle covers a period of one year, with the winter passed in the egg stage upon the trunks and branches of the various host plants. The eggs hatch in late April or early May and maturity is reached late in the summer, the eggs being deposited during the latter part of September and in October.

Observations were made in four localities, namely: Nagasaki in Kyushiu, the southern island, Yokohama and Tokyo in Honshu, and Sapporo in Hokkaido, the northern island, thus covering in latitude a range of approximately 750 miles. The field parasitism of the eggs by *Anastatus* for the four localities is given in Table I, and ranges in effectiveness from 16.3 per cent at Sapporo in 1921 to 34.3 per cent at Tokyo in 1920. A total of 23,015 eggs were collected and set aside for emergence,

and from this number 5,983 adults of *A. albitarsis* were reared, a percentage of 26.0 for all localities during the years 1920 to 1922 inclusive. The host egg-masses often comprised one hundred or more eggs, and in some instances, particularly those collected in the Botanical Garden at Tokyo, the parasitism approached one hundred per cent for individual clusters.

The observations on the life history and habits of this species were undertaken in connection with a comparative

TABLE I.

Anastatus albitarsis Ashm.—Field Parasitism.

1920	Yokohama	Tokyo	Nagasaki
Number of eggs collected	2,500	4,000	2,350
Number of parasites emerged	421	1,373	748
Per cent parasitized	16.8	34.3	31.8
1921	**Yokohama**	**Tokyo**	**Sapporo**
Number of eggs collected	1,560	3,400	2,980
Number of parasites emerged	372	1,069	487
Per cent parasitized	23.8	31.4	16.3
1922	**Yokohama**	**Nagasaki**	**Sapporo**
Number of eggs collected	1,750	1,275	3,200
Number of parasites emerged	502	397	614
Per cent parasitized	28.7	31.1	19.2

study of the biology of the various groups of parasitic Hymenoptera, and the immature forms, particularly the first larval stage, were found to differ to a considerable extent from those known among other species of the same genus and related groups.

LIFE HISTORY AND HABITS.

Oviposition.—The female first examines the host egg leisurely with the antennæ, this often extending in time over five minutes or more, and if satisfied she then takes position on top of it and brings the ovipositor tip forward in a vertical position and in contact with the egg. The tip of the abdomen assists in this process and is then raised to the normal position. The piercing of the shell of the egg requires approximately fifteen

to twenty minutes, and during this time the only movement of the body is a slight rhythmic raising and lowering of the abdomen. After penetration has been finally effected the ovipositor is frequently inserted its full length and withdrawn, and when fully inserted the female rocks forwards and backwards and also somewhat to the side, apparently examining the interior of

TABLE II.

Anastatus albitarsis Ashm.—Oviposition Records, 1922.

Feb.	A	B	C	D	E	F	G	H	I	J
6	1	0	4	1	3	0	4	6	2	3
7	6	3	5	3	5	1	3	3	2	2
8	3	7	5	6	6	5	4	4	5	6
9	5	4	5	2	5	4	6	4	3	5
10	4	3	2	5	5	5	5	6	5	2
11	6	5	7	0	4	2	4	6	5	7
12	2	6	4	8	6	5	4	2	4	4
13	5	5	4	3	6	3	4	5	3	5
14	4	5	6	3	5	6	5	0	6	3
15	7	4	3	3	5	2	3	4	6	4
16	1	3	6	5	5	6	2	3	4	6
17	3	2	2	5	4	3	5	3	5	2
18	5	5	4	2	1	4	1	6	1	6
19	0	4	3	2	D	4	D	4	5	4
20	4	4	4	5	.....	3	.....	4	3	3
21	6	4	D	5	.....	2	.....	2	0	D
22	1	D	.....	D	.....	D	.....	1	2	.....
23	D	.....	.....	.....	.....	.....	.....	D	D	.....
Total eggs	63	64	64	58	60	55	50	63	61	62
Av. per day	3.7	4.3	4.3	3.6	4.6	3.7	3.8	3.7	3.6	4.1
Duration, days	17	15	15	16	13	15	13	17	17	15

D—Female dead.

Average of 10 females.....60 eggs
Average number of eggs per day..... 3.9
Average duration of oviposition period.....15.3 days

the egg with the tip of the ovipositor. She may turn completely about several times during this period, using the fixed ovipositor as an axis. At times she may withdraw it entirely, later returning to complete the process at the same puncture hole. Finally the ovipositor is thrust to its full length and the egg deposited. It is free-floating in the fluids of the host egg. The entire process of oviposition covers a period of thirty to sixty minutes. Frequently the female feeds upon the fluids exuded at the puncture hole. At times the puncture hole in a

parasitized egg may be detected by the presence of the hardened drop of egg fluid which has exuded following oviposition.

The probing with the ovipositor, mentioned above, is apparently for the purpose of determining the stage of development reached by the embryo or the presence of another parasite larva therein. It was not possible to induce oviposition into eggs containing fully developed embryos or parasite larvæ in the advanced stages.

To determine the rate and duration of oviposition a series of twenty-five fertilized females which had been reared out from field-collected material was used for this experiment. The host eggs used were those collected in the field shortly after having been laid in the late summer, and kept in cold storage until needed, so that embryonic development had progressed but little. Ten eggs were provided for each female *Anastatus* per day, and these were later dissected and the eggs contained in them counted. The results for the ten best females are given in Table II. These ten were unusually uniform both in respect to the duration of the oviposition period and in the number of eggs deposited, the former ranging from 13 to 17 days, with an average of 15.3 days, and the latter from 50 to 64, with an average of 60 eggs. From the table it will be seen that the maximum number of eggs laid by a single female in one day was 8, while the average for the entire series was 3.9 eggs. While these experiments were conducted under laboratory conditions it is believed that the results follow quite closely the normal development in the field.

The Larval Stages.—The embryo develops within the egg with its head at the posterior end near the base of the pedicel (See Fig. 2), and may be clearly distinguished through the chorion. The bifurcate process at the caudal end is closely appressed to the body ventrally. Emergence is effected by a break in the chorion at the posterior end near the base of the pedicel in the same manner as described by Phillips and Poos (7) in the case of *Eupelmus allynii*. The larva now lies free in the semi-fluid contents of the host egg, and by means of the ventral rows of spines on the body segments, supplemented by the caudal process, is able to move about in the surrounding fluids. A regular flexing and reflexing of the body permits of the utilization of these structures for that purpose.

The second-stage larva lacks these spines and the long caudal process and is consequently largely incapable of movement, but lies free in the egg fluids. The third stage effects complete consumption of the egg contents before maturity is reached. In the resting condition both ends of the larva are curved ventrally to conform to the shape of the shell within which it is enclosed, the head being always at the posterior end of the host egg. Shortly before pupation the meconium is cast, this being observable as a dark-green, viscid mass placed in the mid-ventral curve of the body. The larva is now bright yellow in color as contrasted with the former mottled green. Shortly before the final moult the developing eyes of the pupa can be seen beneath the derm of the first thoracic segment. The larval skin breaks in a longitudinal line over the head and first two thoracic segments and is forced back over the body, remaining as an irregular ribbon attached to the tip of the abdomen of the pupa.

The Pupal Stage.—The pupa is of the usual form, with both the head and abdomen bent ventrally to fit the outline of the space within which it is confined. The males may be distinguished by the longer antennal sheaths. The only distinctive feature about this pupa is the three prongs superimposed over the ocelli of the developing adult (See Fig. 9). The median prong is longest and directed forwards, while the remaining two point backwards. These prongs may be for the purpose of preventing the head from coming in contact with the shell which encloses the parasite, and are similar to structures found upon the pupæ of many Pompilidæ which are contained in cocoons in the soil. In the latter case their function is obvious, and they are supplemented by similar structures on the thorax and abdomen. Thus moisture penetrating the cocoon does not come in direct contact with the body.

Emergence is effected by the cutting of a hole of rather irregular outline through the upper end of the egg-shell, though occasionally at one side. This hole is not readily distinguishable from that made by the host larva in hatching, though usually slightly smaller.

The Life Cycle.

The cycle of *A. albitarsis* usually covers one full year, the adults emerging during May shortly after the hatching of the

host eggs. The males precede the females by an average of three days, and the two sexes appear in numbers in the ratio of 1 to 1.4, the females predominating. Mating takes place almost immediately. In case of parthenogenetic reproduction the progeny are all males. The females are very active and capable of jumping great distances; in fact, this rather than flight is their chief mode of movement from place to place. In jumping the abdomen is bent sharply backwards over the thorax, and in alighting the female frequently tumbles about somewhat before gaining a foothold. This corresponds quite closely to the account given by Riley of (*Eupelmus*) *Anastatus mirabilis* (Walsh and Riley), "the back-rolling wonder."

The length of life of the adult female is from five to six months, extending from May to October or November, at which time freshly deposited host eggs are available for oviposition. The males die shortly after mating. No intermediate host is known.

The egg stage covers a period of three to five days, dependent upon temperature conditions, and the mature larval stage is reached within one month. It is in this condition that hibernation takes place. The pupal stage is short, extending over about two weeks.

While one generation per year is the normal condition, yet there is evidence to show that a partial second occurs in the infertile eggs of the same host generation in the spring, and this was demonstrated experimentally in the laboratory. *A. albitarsis* is a true egg parasite, as has already been pointed out, and develops free-floating in the egg fluids rather than in the body of the developing embryo. Laboratory tests to determine to what extent development is possible in eggs of various stages of maturity showed that oviposition and normal development took place only so long as the egg cavity surrounding the growing embryo was filled with fluid. The egg was never deposited within the embryo. This same condition was found to hold true with respect to several other species of the same genus which were studied.

Description of Immature Forms.

The Egg (Fig. 2). Total length, 0.68 mm., the main body being 0.5 mm. in length and 0.11 mm. in width, slightly curved as shown in the figure, and widest towards the posterior end. At the anterior end is a minute tubercle, while the opposite end bears a large, prominent

pedicel 0.18 mm. in length, which is firm and turgid at all stages of development. The chorion is heavy, firm and without sculpturing. Color white, and granular when viewed by transmitted light. The mature ovarian egg is of similar size and form.

The First-Stage Larva (Figs. 3 and 4). Length to tip of caudal process, 1.2 mm., width, 0.2 mm.; body form as shown in the figures, the segments very distinct and diminishing in diameter caudad.

Head robust, thimble-shaped, heavily chitinized, and slightly brownish in color; one pair of short setæ situated ventrally and near the middle; the buccal area rather large, with the mandibles simple and dark in color.

Body segments thirteen in number, distinct, and approximately equal in length except the last, which is much extended into a heavily chitinized, bifurcate process, the points of which are very sharp. The "prongs" of this process are sharply curved at the base and lie at right angles to the body axis. Between the base of these and the anterior ventral margin of the segment is a pair of short, stout protuberances. The second and third thoracic segments and the first seven of the abdomen bear ventrally near the anterior margin a row of twelve to fifteen long, heavy spines, those on the second thoracic segment being very long, and diminishing in length on the successive segments. The spines on the median line are longest, the others diminishing in length laterad. Neither the bifurcate structure nor the two smaller supplementary processes bear spines or setæ of any sort. Body color white, with the digestive tract distinctly visible through the derm.

The tracheal system comprises four pairs of open spiracles, these being situated on the second thoracic and the first three abdominal segments respectively, and the lateral trunks are connected by posterior and anterior commissures.

The Second-Stage Larva (Fig. 5). Head similar in form to that of the first stage but relatively much smaller, with one pair of setæ situated ventrally.

Body segments thirteen in number, with the first abdominal segment widest, and diminishing anteriorly and posteriorly. The thoracic and abdominal segments about equal in length and distinct, the last segment bifurcate, but lacking the heavily chitinized prongs of the preceding stage. Three pairs of cuticular spines on each of the thoracic segments and two on each abdominal segment except the last.

Tracheal system with eight pairs of open spiracles.

The Third-Stage Larva (Fig. 9). Length extended, 2.5 mm., and width, 1.0 mm. Body distinctly segmented and robust. Color a mottled green and white, the green due to the contents of the digestive tract showing through the derm and the white to the numerous irregularly shaped fat bodies lying near the surface. The green is most noticeable in the median abdominal area.

The head (Fig. 7) is small and somewhat retracted, with two prominent tubercles representing the antennæ situated on the transverse median line. Four pairs of sensory setæ are present, one situated slightly mesad and above the antennæ, the second slightly laterad and

above, the third directly laterad and the fourth laterad of the buccal aperture. Two pairs of heavy greenish lines extend from the posterior margin of the head nearly to the antennæ, those of each pair uniting and again separating just before reaching the antennæ. The latero-ventral portions of the head are greenish-black in color. The mandibles are simple, sharp, and black in color distally.

The thirteen body segments are distinct and of nearly equal length except the last, which is shorter. The first thoracic segment bears two pairs of cuticular spines, and the second and third three, while the abdominal segments from the first to the seventh bear two. The derm of the lateral margins of the second and third thoracic segments, and dorsally on the first seven segments of the abdomen as well, with fine, irregularly linear granulations, being slightly darkened in color on the thoracic segments and in the spiracular areas.

The tracheal system comprises nine pairs of open spiracles situated on the second and third thoracic and the first seven abdominal segments.

The Pupa (Fig. 8). Length, 1.4 mm., with the head appressed ventrally and the abdomen curved likewise, the central body axis thus being practically a semicircle. Head with three fleshy prongs situated over the developing ocelli (Fig. 9), the median one directed forwards and the two laterals pointing caudad. The color ranges from white in the newly transformed individuals to black just prior to emergence, the iridescent reflections from the thorax being then visible through the pupal integument.

The Primary Larva of A. albitarsis Compared With Others.

The features in which the primary larva of *A. albitarsis* differs from that of other Chalcidoidea are the transverse rows of long, heavy spines ventrally on certain of the body segments and the long, heavily chitinized bifurcate process terminating the caudal segment. In most of the forms of caudate larvæ among the parasitic Hymenoptera the last segment is prolonged into a large fleshy process, which is unquestionably respiratory in function. Typical of this form are the Braconidæ, some Ichneumonidæ, certain Aphelinidæ, Chalcididæ, various Encyrtids, etc. The bifurcate appendage of *A. albitarsis* is similar in all essential respects to that found upon the primary larvæ of various Proctotrypoid egg parasites (Scelionidæ), and in neither case can its function be considered as respiratory. It is worthy of note that many of the most remarkable morphological modifications among the primary larvæ of the parasitic Hymenoptera are found among those parasitic within the eggs of other insect species. It is probable that the bifurcate appendage

mentioned was originally ambulatory in function and still serves in this way to a limited extent, though in a fluid medium rather than upon an external surface.

In a recent paper Parker (5) discusses at length the post-embryonic development of the Chalcidoid Hymenoptera, and has classified the primary larvæ morphologically into seven groups. *Anastatus* was not figured therein, but slightly later Parker and Thompson (6) published an account of the primary larva of *Anastatus* sp. which they consider to be a transitional form between the free-living endophagous larvæ, typified by *Ceraptorocerus mirabilis* Westw., and the ectophagous larvæ of the group including *Leucospis*, *Eupelmus*, *Eurytoma*, etc. The larva described bears numerous cuticular spines, though not localized ventrally, and a short bifurcate caudal process. The larva of *A. albitarsis* is of a more primitive type than that described by Parker and Thompson. All of the caudate forms discussed, in which the process is bifurcate, have these processes very short, and in none of them is there any indication that they have a respiratory function. It is possible that among the Hymenoptera the two caudate forms are of entirely different origin, the simple being respiratory and the bifurcate ambulatory. It is noteworthy that in certain widely separated groups of parasitic insects, the primary larvæ of which are under the necessity of searching for their hosts, nearly all bear on the caudal segment a pair of strong setæ of greater or less length. As typical of these may be cited the Perilampidæ and Eucharidæ among the Hymenoptera and the Acroceridæ, Bombylidæ and Dexiidæ among the Diptera.

The hypothesis presented by Parker and Thompson that *Anastatus* is a form which recently has adopted the habit of endophagous parasitism and is now undergoing the changes incident to such transformation of habit may be considered as strengthened by the further evidence adduced in the case of *A. albitarsis*.

Host Relationships of the Genus Anastatus.

A review of the published records of the hosts of this genus reveals it to be confined very largely to the eggs of four orders of insects, namely: Lepidoptera (*Nymphalidæ*, *Lymantriidæ*, *Lasiocampidæ*, and *Saturniidæ*), Orthoptera (*Blattidæ*, *Mantidæ*,

Acrididæ and *Locustidæ*), Hemiptera (*Pentatomidæ* and *Coreidæ*) and in a single instance from a Neuropteron (*Torbia viridissima*). An exception to this *A. pipunculi* Perkins, recorded as being parasitic in the sacs of the Dipteron *Pipunculus cinerascens* and also in those of *Paradryinus* sp., belonging to the hymenopterous family *Dryinidæ*, both parasitic upon leaf-hoppers in Australia. In Ceylon *A. tachardiæ* How. is reported as parasitic upon the lac insect (*Tachardia albizziæ*), but in view of our knowledge of the habits of the genus the record must at present be considered as questionable. The doubtful record of *A. aureicorpus* Girault from a single Syrphid puparium in Texas is almost certainly erroneous.

Aside from lepidoterous eggs the writer has reared species of this genus most commonly from the eggs of *Pentatomidæ* and *Coreidæ*, and it is probable that the eggs of other families of the order, of which the species have similar habits and are of sufficient size, are also attacked.

Literature on the Biology of the Genus Anastatus.

No complete account has been published to date on the life history of any species of the genus *Anastatus*. That of *A. bifasciatus* Fonsc., the imported egg parasite of the gipsy moth, is treated in a general way by Howard and Fiske (3) and Crossman (2), but the early stages of the larva are not described or figured. One generation per year is produced.

In 1921 Caffrey (1) published an account of the life history of *A. semiflavidus* Gahan, parasitic in the eggs of *Hemileuca oliviæ* Ckll., but in this case also the early larval stages are not discussed. The normal life cycle is stated to cover one year, though a portion of the generation prolongs the mature larval stage to the second year. This aestivation through an entire additional season is doubtless due to the extremely low humidity occurring during the time at which emergence takes place. This is similar in effect to the reactions of insects in tropical sections where no rainfall occurs during the winter months and atmospheric humidity is very low, development during this period being suspended in spite of the relatively high temperatures.

In discussing the irregular life cycle Caffrey also states that a portion of the eggs probably pass the winter as such, and that those deposited early develop partially and then reach the mature larval condition early in the spring. Considering the very short incubation period known for other species of the genus it is quite improbable that the eggs do carry over the winter, and the more normal condition is for the mature larval stage to be reached quickly, and before hibernation.

The sex ratio of *A. semiflavidus* was found to be 1 to 1.4 and 1 to 1.5, the females predominating, in the two series in which counts were made, and this is practically identical with that noted by the writer for *A. albitarsis*.

In two additional species of *Anastatus* reared by the writer from Pentatomid eggs in India during the past season the primary larvæ were identical in form with that figured by Parker and Thompson. The fleshy prongs upon the head of the pupa were lacking in these two species, as they are also in *A. bifasciatus* and *A. semiflavidus*.

Of the related genus *Eupelmus* accounts have been given of *E. allynii* French, parasitic externally upon *Harmolita tritici* Fitch and its other parasites, by Packard (4) and Phillips and Poos (7), and of *Eupelmus* sp. by Parker (5). The egg of *E. allynii* has a sharply pointed pedicel at the anterior end, while the long pedicel at the opposite end is delicate and collapses after the egg is laid. The primary larvæ of the above species, being external feeders, differ in form from that of *A. albitarsis* in lacking both the long ventral setæ on the body segments and the large bifurcate caudal process.

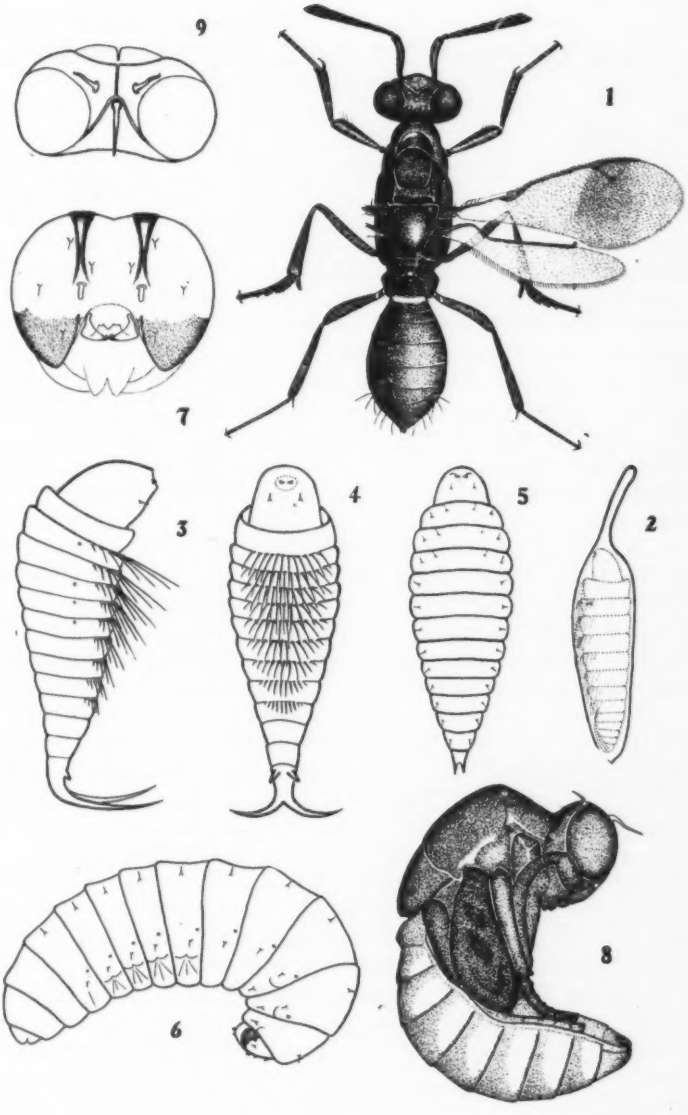
LITERATURE CITED.

1. **Caffrey, D. J.** 1921. U. S. D. A., Jl. Agric. Res., Vol. XXI, No. 6, pp. 373-384.
2. **Crossman, S. S.** 1925. U. S. D. A., Jl. Agric. Res., Vol. XXX, No. 7, pp. 643-675.
3. **Howard, L. O.**, and **Fiske, W. F.** 1911. U. S. D. A., Bur. of Ent., Bull. 91, 334 pp.
4. **Packard, C. M.** 1916. U. S. D. A., Jl. Agric. Res., Vol. VI, No. 10, pp. 367-382.
5. **Parker, H. L.** 1924. Ann. Soc. Ent. France, 1924, No. 4, pp. 261-379, pls. 2-39.
6. **Parker, H. L.**, and **Thompson, W. R.** 1925. Ann. Ent. Soc. Amer., Vol. XVIII, No. 3, pp. 384-395.
7. **Phillips, W. J.**, and **Poos, F. W.** 1921. U. S. D. A., Jl. Agric. Res., Vol. XXI, No. 6, pp. 405-426.

EXPLANATION OF PLATE XXIII.

Anastatus albitarsis Ashm.

Fig. 1. Adult female. (× 25).
Fig. 2. The egg, showing larva just before hatching. (× 65).
Fig. 3. First stage larva, lateral view. (× 90).
Fig. 4. First stage larva, ventral view. (× 90).
Fig. 5. Second stage larva, ventral view. (× 50).
Fig. 6. Third stage larva, lateral view. (× 35).
Fig. 7. Head of third stage larva, anterior view.
Fig. 8. Pupa, lateral view. (× 40).
Fig. 9. Head of pupa, dorsal view.



Curtis P. Clausen

THE AMERICAN CATOPSILIAS (LEPIDOPTERA, PIERIDÆ).

WM. T. M. FORBES,
Cornell University, Ithaca, N. Y.

The Rhodocerid group of Pieridæ fall into three sub-groups. One, composed of *Eurymus* (Colias) and *Meganostoma* is characteristically holarctic, and has invaded the tropical zone of both hemispheres only along the mountains. The second composed of *Dercas*, *Eurema* (Terias), *Teriocolias*, and *Nathalis* appears to have its most primitive forms in the tropics of the old world, though this is not quite certain, the typical genus Eurema being far more varied in America than in the old world. The third group, *Catopsilia*, *Kricogonia*, and *Gonepteryx*, is obviously tropical American, all the genera occurring in America, and only two limited groups of species having invaded the old world.

The genus Catopsilia was last reviewed as a whole by Butler in the Lepidoptera Exotica. Seitz's Macrolepidoptera of the World is hardly more than an illustrated catalogue in this genus, and makes no attempt at revision of the American names. It seems that a grouping of the species on structural characters and a key to the species might be useful.

The genus, as usually limited, falls into seven well-defined groups on the secondary sexual characters of the male; one of these including all the old-world species, while the rest are limited to America. To these I would add "*Gonepteryx*" *menippe*, as it is closely related to the old-world group of Catopsilia, and violates the definition of the otherwise homogeneous Gonepteryx. It might well be made one of the Old World group, with which it agrees in markings of the under side, as well as fairly well in sexual characters, but I have thought best to let it form an eighth group by itself. The groups form a fairly good linear series, but this arrangement is not a strictly evolutionary one. It would appear from the simplicity of secondary sexual structures and completeness of pattern (in sennæ), that the eubule group is perhaps most primitive.

Following are the groups:

A: **philea.** Mealy border extending almost to bases of cells down to M_2 or even M_3, then abruptly narrowed and marginal only from there down, also invading cell and extending in far toward base on inner margin. No hair-pencil. Sex patches on both wings where they overlap (easily seen by holding the butterfly to a bright light).

B: **eubule** (Callidryas). Mealy border similar, but with the abrupt decrease in width coming higher, the border being narrow in cell M_2 and sometimes even in R_5 and M_1, not invading cell. No hair pencil, no sex-patches.

C: **argante** (Phoebis). Mealy border all very narrow, not approaching the cell even on the costa; extended in on inner margin, especially narrow on hind wing. Hind wing with a hair-pencil but no sex-patch. Wings rounded.

D: **neocipris** (Metura). Similar, but the border very broad and even in width. Hind wing tailed at anal angle.

E: **trite** (Rhabdodryas). Border evenly broad, but little extended in on inner margin. Hind wing with a fringe of hair and a double sex-patch, riding on vein R, the fore wing without fringe or sex-patch.

F: **statira** (Aphrissa). Mealy border broad and even, about as in **trite,** but frequently invading the cell; ending abruptly on hind wing near Cu_1. No hair-fringe; sex-patches when present similar on both wings, rarely wholly absent, or indicated by an evanescent thickening.

G: **crocale** (Catopsilia). Mealy area covering almost whole upper surface of fore wing, and covering more than half of the cell, as in Kricogonia and Gonepteryx. Inner margin of **fore** wing with a fringe of hair, the hind wing without, but with a stigma. Old-world species, typically with a streak on under side of hind wing along top of cell, the costal region paler, as in Gonepteryx.

H: **menippe.** Mealy area confined to a large patch on **dorsal** half of wing, the apex plain. Hair-pencil on fore wing rudimentary, but with the lobe which should bear it particularly well marked. Hind wing with large sex-spot and broad mealy border.

Key to the Species and Forms (Male).

A. Group *philea.*

1. Mealy area in cell M_2 extending nearly to its base, sometimes with a spot on the basal part of cell Cu_1 also; fore wing with a black discal dot, the orange or red oblique band larger below than in the cell (Antilles).....2
1. Mealy area in cell M_2 short, like those below; fore wing without a black discal dot, the orange band with part below cell of smaller area than part in cell (Mainland).....***philea**
2. Fore wing with anal angle more extended, under side with ground yellow, contrastingly marked and blotched with brown; upper side of wings with yellow and orange, but no red.....***thalestris**
2. Fore wing more rounded; under side evenly and usually heavily dusted with dull red, without brown blotches; upper side extensively marked with vermillion.....***avellanada**

B: Group *eubule*.

1. Mealy border narrower toward costa, the basal half of cell M_1 and frequently much of cell R_5 also, clear. Under side of hind wing usually immaculate or nearly so, (Atlantic States).....***e. eubule**
2. Mealy border nearly filling cells R_5 and M_1. Under side of hind wing normally with almost the complete maculation traceable, (Miss. Vall. to S. America, also Antilles).....***e. sennæ**

The two subspecies appear to intergrade in the greater Antilles. *C. drya* is usually identified as a small form of *sennæ* from Chile. I am not sure that the form is distinct enough to have a name, as many Antillean specimens are no larger; and also the name *drya* probably does not belong to it. The discal dot of the fore wing below averages smaller in Chilean forms, even as compared with Antillean specimens of the same size.

C: Group *argante*.

1. Postmedial series of spots on under side of fore wing continuous, frequently represented mainly by a band of dark dusting.....***agarithe**
1. Postmedial spot in cell M_3 well defined and far near margin than that in cell M_2 (*argante*).....2
2. Terminal black line of fore wing above continuous, at least toward costa, ab. ***hersilia**
2. Terminal series of black points only.....***typical**

There appears to be some difference between Antillean and Mexican specimens of *agarithe*, at least in the female, where I have made a distinction in the key.

The S. Domingo race of argante (*rorata* Btl.) also is easily distinguished in the female. I have seen no males, and do not know how to separate it from typical argante. *Hersilia* is a partly racial form, apparently being more common on the mainland.

D: Group *cipris*.

1. Expanse over 70 mm.; base of fore wing sulphur yellow, only a little darker than the mealy border.....***c. rurina**
1. Smaller, expanse under 70 mm.; base of fore wing bright orange yellow, contrasting.....***c. cipris**

These two forms appear to intergrade perfectly, and are not really even of racial value. They may be kept as dimorphic forms.

E: Group *trite*.

***C. trite** only. A very distinct and constant species.

F: Group *statira*.

1. Areas of sex-scaling on inner margin of fore wing and costa of hind wing long-elliptical, bluntly pointed at outer end. Fore wing above with a large nearly circular orange area on the basal half, contrasting with the lemon yellow at the apex of the cell and whiter mealy border.....**†orbis**

1. Areas of sex-scaling on overlap of fore and hind wings shorter, rounded-triangular, with truncate outer ends (rarely obsolete). Fore wing above with basal part wholly of one color, yellow or cream.....2
2. Under side with more or less distinct postmedial markings on both wings, (*godartiana*).....3
2. Under side immaculate.....4
3. Pattern below nearly complete; upper side lemon yellow.....**g. godartiana**
3. With postmedial markings reduced to a series of dots; upper side tinted with orange.....**g. hartonia**
4. No sex-marks at overlap of fore and hind wings; mealy border purer white than usual, under side pale, especially toward marginal half of hind wing.....***etiolata**
4. Sex-marks sharply defined, a little weak in *wallacei*, which has a yellow mealy border.....5
5. Yellow with white border; mealy area with a spot in end of cell (one specimen from Itaituba wholly white).....***statira**
5. Wholly yellow, the border only slightly paler; typically without any mealy spot in cell.....***neleis** (Antilles); ***wallacei** (N. South America)
5. Evenly pale buff or cream color, the border practically concolorous; mealy border of hind wing very broad.....***boisduvalii**
5. Similar, the basal part of the wing distinctly tinted with orange.....**jada**

G: Group **crocale.*

This group contains five or six old-world species, with numerous forms.

H: Group *menippe.*

This group contains the very distinct **C. menippe* only. It is generally put in Gonepteryx, and is perhaps actually a transition to that genus, but it lacks the usual angle on the hind wing, and seems not at all out of place in Catopsilia, where it is really close to florella.

Artifical Key To Females

The following key is tentative and to a certain extent incomplete, but may serve as a guide. Females of Catopsilia are highly variable, especially in color, but also to a considerable extent in markings; and are also relatively rare both in collections and in the field. They are rarely taken in association with the males, and in the statira group we cannot yet safely match the various female types with their corresponding males. Butler attempted to do so, I think with partial success, and I have generally followed him. As to color, yellow and white females occur in almost every species, and orange ones also in the cases where the male is orange. There is also the orange C. jaresia Btl., (Pl. 51, Figs. 5, 6) which evidently belongs either to statira or the similarly colored etiolata, as those two species occur at the same place. As the markings are identical with undoubted statiras, from points where etiolata seems absent,

in fact with Cramer's figure of the type, I suppose it is a color form of statira.

1. Very large; apex of fore wing shaded with orange; under side of hind wing with a pale shade along R.....***menippe**
1. Smaller; apex not shaded with orange; costal part of hind wing not specially marked.....2
2. Hind wing tailed (*neocipis*).....3
2. Hind wing rounded.....5
3. Small, ground evenly yellow.....***n. neocipris**
3. Larger; ground with white or red or both †*n. rurina*.....4
4. Yellow, marginal part of hind wing broadly shaded with red.....**†typical**
4. Border narrow and more or less broken into a series of spots....var. **intermedia**
4. White, without red border.....var. **†virgo**
5. An even, continuous, sharply defined median line on hind wing, besides postmedial markings, and postmedian line on fore wing.....***trite**
5. No continuous dark line across the wings.....6
6. Under side of fore wing with postmedial spots ending abruptly at M_3; upper side normally with a continuous border extending below Cu_1, as well as a discal dot, but without postmedial markings (group *statira*).....15
6. Under side usually with a complete series of spots. Fore wing above with distinct postmedial spots, or else with the black border cut up into spots on the veins; (the pm. spots frequently partly fused with the border in *arganta*).....7
7. Postmedial series of spots on fore wing (visible at least beneath), continuous, with the spot in M_3 slightly farther from the margin than in M_2, **†agarithe**[2]
7. Postmedial spot below M_3 much closer to margin than that above M_3; in most cases (except group philea) only half as far from margin as the next one below it.....8
8. Discal dot of fore wing below always with a distinct portion lying above the origin of vein M_1, when the spot is large with this upper portion nearly as large as the lower. Spot in cell M_1 below only a little nearer margin than that in Cu_1, (group *philea*).....9
8. Discal dot normally small and wholly below M_2; rarely enlarged, but in that case with the part below M_2 several times as large as the part above, which may be a mere dot. Spots in cells M_2 and M_3 very obliquely placed.....12
9. Fore wing with border continuous and broad at apex; the outer margin practically straight; border of hind wing normally shaded with red..***philea**
9. Border weaker and broken into spots: outer margin strongly concave at middle.....10
10. Large; hind wing more or less suffused with red, sometimes almost wholly, but with paler base.....11
10. Smaller; hind wing with ground color nearly even; orange or yellow in the specimens examined.....**†thalestris** (S. Domingo race)[3]
11. Under side of hind wing ochre yellow with contrasting dark brown markings and shadings.....**†thalestris**
11. Under side of hind wing with ground color evenly dusted with red, usually heavily, the markings not contrasting.....**†avellanada**
12. Apex typically with a black patch involving the postmedial spots in cells R_3 and R_5, the spot in cell M_1 often also connected; if reduced with the border of the hind wing reduced to small dots.....(**argante**) 13
12. Apex with a narrow border, separate from the postmedial spots, save in occasional specimens which have a complete border on the hind wing, (*eubule*).....14

---

[2]The typical form is heavily marked with black on the upper side, much like **C. argante**; in the Greater Antilles there is a female with the black much reduced, the border mainly represented by a small apical spot, and small terminal dots below (**floridensis**). This is the form which Butler figures as agarithe.

[3]This is editha ♀ of Butler.

13. Ground orange, yellow or white, with little or no red dusting.....*a. **argante**
13. Ground heavily dusted with deep Indian red.....†a. **rorata**
14. Under side with all the markings small and well separated; upper side normally with discal dot on fore wing the most conspicuous mark..*e. **eubule**
14. Under side with markings heavy and connected, frequently also dusted with reddish; upper side with border strongly developed, the discal dot less conspicuous.....*e. **sennæ**
15. Upper side of fore wing with postmedial dots above M_3.....**orbis**
15. Upper side without postmedial dots or with traces of tawny ones.....16
16. Upper side of fore wing with well marked black border, but no discal dot at all.....†**wallacei** (supposition)
16. Discal dot distinct.....17
17. Discal dot moderate in size, and limited to the lower disco-cellular vein; black border traceable on hind wing as well as strong on fore wing, *__statira__ 18
17. Discal dot large, and resting on the middle as well as the lower disco-cellular, sometimes the whole height of the cell; a little smaller when the border is reduced to a slender line on the fore wing only.....19
18. Ground orange.....*ab. **jaresia**
18. Ground yellow or ochreous, much paler on marginal half.....*__typical__
19. Ground wholly buffy cream, concolorous with male.....†**boisduvalii**
19. Basal half of wing bright yellow, or orange.....20
20. Solid bright yellow; border reduced to dots.....†**neleis**
20. Yellow, border continuous.....21
20. Much shaded with orange; border very heavy.....**godartiana**
21. Discal dot on lower dcv. only; border almost enclosing a yellow subapical spot.....**jada**
21. Discal dot extending up on mdcv. border entire.....**hartonia**

Descrihtion

C. etiolata new species

Closely similar to *C. statira* and usually confused with it. Mealy border narrower, usually reaching close to the lower angle of the cell, but rarely with a spot within the cell, sex spots on inner margin of fore wing below and costa of hind wing above, very obscure, without definite boundary and barely visible when the specimen is held against a strong light. Color and markings almost identical with *C. statira*, except that the narrower mealy border is plainly shown as a narrower pure white outer half of the wing, the cell being wholly yellow. Hind wing beneath paler than in *statira*, typically light yellow at the base, gradually shading into cream white at the outer margin. 55mm.

Holotype and several paratypes from the Lower Pachitea River, Eastern Peru, July 22, 1920; Cornell University, Lot 607, Sub 143, type No. 835; also paratypes from Puerto Bermudez, Rio Pichis, Peru, July 17; Azupizu, Camino del Pichis, Peru, July, San Carlos (Mapiri), Bolivia (O. Buchtien coll.); Itaituba and Santarem on the lower Amazons (H. H. Smith); Chanchamayo District, Peru (Sarco); Serra Cantareira, S. Paulo, Brazil, Mar. 1903 (Hammar) (not typical). A specimen labelled as from New Mexico is probably in error (Foulks Coll.). The species is also in the American Museum of Natural History from Venezuela, and is probably generally confused with *C. statira*.

It would appear that this is a distinct species, considering the difference of structure, and the considerable number of like specimens. There are, however, a few specimens that seem to show intergrading or hybridization with *C. statira*, either showing the lack of sex-patch with the narrow mealy border (Itaituba, Amazons, H. H. Smith) or a broad mealy border entering the cell, with the intense white color of this species and no sex-patch (Yurimaguas, Peru, Mar. 25, 1920, H. S. Parish) or else the deeper buff under side (Colombia and R. Uaupes, N. W. Brazil, in American Museum). *C. wallacei* is also very near, and was apparently confused with this form by Butler, who figured it with the characteristic pale under side of this form; but the series which I identify as *wallacei* (From Kartabo, British Guiana) have a decidedly yellow border, and a definite though not conspicuous pair of stigmata, they also have the deeper yellow under side of the original description.

I have not recognized the female, it may be *jaresia* Butler, which H. H. Smith took in association with *statira* and *etiolata*, or the form which I have entered in the key as possibly the female of *wallacei*.

LIST OF NAMES.

A. **philea.**

1. philea
   syn. ♀ *forna*
2. thalestris
   a. editha (♀)
3. avellanada
   syn. solstitia

B. **(Callidryas) eubule.**

4. eubule
   a. sennæ
   syn. marcellina
   syn.? drya
   syn.? editha ♂
   syn. ♀ *cipris Cr.*
   ♀ ab. yamana
   syn. pallida

C. **(Phoebis) argante.**

5. agarithe
   a. floridensis
6. argante
   var. hersilia
   ab. minuscula
   a. rorata

D. **(Metura) neocipris.**

7. neocipris
   syn. cipris F.
   a. rurina
   ♀ ab. virgo
   ♀ ab. intermedia

E. **(Rhabdodryas) trite.**

8. trite

F. **(Aphrissa) statira.**

9. statira
   syn. ♂ *alcmeone*
   ♀ ab. jaresia
10. etiolata
    syn. wallacei Btl.?
11. wallacei Fld.
12. neleis
13. godartiana
    a. hartonia
14. boisduvalii
    syn. butleri
    a. jada
15. orbis

G. **(Catopsilia) crocale.**

16. pyranthe
17. florella
18. crocale
19. pomona
20. scylla

H. **menippe.**

21. menippe

THE EXTERNAL ANATOMY OF THE LARVA OF HOPLOCAMPA HALCYON NORT. WITH A KEY TO THE INSTARS AND TO THOSE OF RELATED SPECIES (TENTHREDINIDÆ, HYMENOPTERA).*

By Ralph D. Bird.

The following account is based on a series of larvæ bred by the writer while studying the life histories of sawflies in southern Manitoba. The species concerned are, the Saskatoon sawfly (*Hopocampa halcyon* Nort.) which breeds in the fruit of *Amelanchier spicata*, and *Hoplocampa xantha* Rohwer and *Hoplocampa* (*MacGillvrayella*) *lacteipennis* Rohwer both of which as larvæ bore in the fruit of *Prunus virginiana* (1, 2).

Until more specimens of the larvæ of the subfamily Hoplocampinæ (Hemichroini) Rohwer (3) are available for study it will be impossible to make a key to separate the genera. The species studied run to the genus *Marlattia* in Yuasas key (4) to the Hoplocampinæ, but they may be separated from this genus by the pigmentation of the anal segments and the total lack of coloration of any areas not heavily chitinized.

In order to bring out the external characters of the larvæ of the genus *Hoplocampa* a study was made of the fifth instar of *H. halcyon* Nort. and characters found to be of specific value for separating the species concerned are shown in the comparative table and key. Special attention was paid to the spines on the lacinia, epipharynx and front, but they were found to be variable and of no specific value as was also the shape of the labrum.

In general it may be said that the larvæ studied typically have five annulets on the abdominal segments; two large setæ on the labrum; very short, conical, three-segmented antennæ; two-segmented labial and four-segmented maxillary palpi, and pigmented areas on the dorsum of the anal segments. All are borers in fruit.

*Contribution No. 114, from the Entomological Laboratories, University of Illinois, Urbana, Illinois.

The External Anatomy of *Hoplocampa halcyon* Nort.

The larva of *Hoplocampa halcyon* Nort., like those of all the Tenthredinidæ, with the exception of the leaf-miners is cylindrical in form and caterpillar-like. It has a sub-globular head and a series of thirteen well defined segments. Its thoracic legs are well developed. In addition its ten-segmented abdomen bears a pair of fleshy protuberances or prolegs on the latero-ventral aspect of segments two to seven and ten. These differ from those of the lepidopterous larvæ in the absence of a circlet of terminal hooks or crochets.

The head.—(Figs. 3, 5 and 11). The head capsule is brown, slightly roughened and is covered with a few short setæ. It bears an inverted Y-shaped median epicranial suture. The stem of the "Y" (ES) originates at the occipital foramen, extends cephalad, dividing the vertex into two halves and bifurcates in a central position of the cephalic aspect of the head. Each arm (EA) of the bifurcation after extending obliquely laterad for a short distance then bends ventrad to the ventral margin of the capsule where it terminates near the subtriangular clypealia (CL). The dorsal, lateral, and the greater part of the cephalic and caudal aspects of the head form an area, the epicranium, which is subdivided into three definite areas, the vertex (V), the genæ (G) and the front (F).

The vertex (V) extends from the stem of the epicranial suture to the ventral margin of the head, laterad of the epicranial arm and cephalad of the occipital suture (OS). It bears an ocularium (O) and an antennaria (A). A vertical furrow (VF) extends on each side of the vertex from the occipital foramen cephalad for a considerable distance on the lateral aspect of the head.

The genæ (G) occupy that portion of the vertex ventrad of an imaginary line drawn ventrad of each ocellus parallel to the ventral margin of the head capsule.

The front (F), that area on the cephalic aspect of the head bounded by the epicranial arms, is pentagonal and as long (dorso-ventrally) as wide (laterally). It is slightly concave and bears a few setæ which vary with the individual.

The ocularіæ (O) are situated, one on each side of the head at about their own width dorsad of the antennæ. They are round, black and bear in their center a clear semiglobular ocellus.

The antennæ are situated near the center of a whitish, oval antennaria (A). They are composed of three joints, the first of which is incomplete ventrally. They are very short and each about one half the diameter of the preceding.

The clypeus is a narrow sclerite bounded dorsally by the fronto-clypeal suture (FC) and ventrally by the clypeo-labral suture (CLS). Its lateral margins are free and converge ventrally at an obtuse angle. It is divided into a preclypeus (PE) and a post-clypeus (PO) by the clypeal suture (CS).

The lobe-like labrum (L) has a shallow, broad emargination on its ventral margin. Two lateral setæ are borne on each side of the meson.

The postgenæ (PA) include those areas between the occipital suture and the body of the tentorium (MT).

The feebly developed maxillariæ (MA) bound the dorsal margin of the oval occipital foramen (OF).

The mouthparts.—The larvæ of *Hoplocampa halcyon* like those of other Tenthredinoidea possess well developed mandibulate mouthparts consisting of a pair of mandibles, a pair of maxillæ and a labium.

The mandibles (M and Fig. 8) are short, thick and strongly chitinized. They bear at their distal end four dentes, the two lateral ones of which are much smaller than the two mesal ones.

The maxillæ (MX and Fig. 9), as is typical consist of a cardo, stipes (S), palpifer (PF), palpus (MP), galea (GL) and lacinia (LA). The cardo is divided into a large alacardo (AC) and a small subcardo (C). The alacardo is a rhomboidal sclerite articulating with the stipes on its latero-proximal aspect. The subcardo is a small triangular sclerite at the proximal end of the alacardo. The stipes which constitutes by far the largest part of the maxilla is not as heavily chitinized as the cardo. It is convex on its lateral aspect, while the cephalic aspect is membranous and continuous with the maxacoria. Along the mesal aspect of its caudal margin it is fused to the elongate subgalea (SG) by a distinct chitinized ridge which extends from the lateral margin of the alacardo to the lacinia. The palpifer at the cephalic margin of the stipes is sub-globular and bears two large setæ on its lateral aspect. The maxillary palpus (MP) consists of four, conical segments of approximately the same length but successively smaller in diameter. On the disto-mesal margin of the third segment there is a row of four setæ. The galea (GL) is a blunt, unsegmented projection smaller than the maxillary palpus and curved mesad slightly. The lacinia (LA) is flattened and bears a row of five to seven setæ on its distal edge.

The labium (LI and Fig. 10), consists of submentum (SM), mentum (ME), palpifer (PF), a pair of labial palpi (LP) and a subglobular lobe (HX) representing the fused glossæ and paraglossæ. The mentum (ME) is large and has six prominent setæ, two just below each palpifer and one on each lateral margin. The submentum (SM) merely consists of a band-like chitinous area separated from the mentum by a membrane equal to it in width. The palpiger (PG) is well developed and the palpi consist of two conical segments.

The prepharynx (hypopharynx) is a simple lobe-like organ situated between the laciniæ of the maxillæ. As it is not strikingly modified in the various families of the Tenthredinoidea (4) it is not figured for this species.

The epipharynx (Fig. 4) bears a characteristic group of setæ the number and shape of which are variable with the individual.

The cervacoria is the membranous area connecting the head and prothorax. It is supported on each side by a triangular, brown, cervical sclerite not shown in the figures.

The thorax.—(Fig. 3), is only feebly chitinized and is strongly declivitous on the dorsal aspect, which is divided more or less completely into four annulets in each segment. The metathorax and pro-thorax bear spiracles (SPI), the latter supposedly a mesothoracic spiracle which has moved forward.

The thoracic legs.—(Fig. 7). Each segment of the thorax bears a pair of typical, well developed legs consisting of five segments, coxa (CX), trochanter (TR), femur (FM), tibia (T) and a distal segment (CW) representing the fused tarsus and tarsal claw (Yuasa).

The abdomen.—(Figs. 1, 2 and 6), is cylindrical, glabrous and bears a pair of prolegs on segments 2-7 inclusive and 10. All but the last three segments are subdivided into five annulets. The most typical segment is the third (Fig. 2) which also bears well developed subspiracular (SL) and surpedal (SP) areas and is annulated on the sternum as is shown in figure 6. No ventral glands were found. The terga of the eighth, ninth and tenth segments are not annulated, but are heavily chitinized and spotted with black. There is no suranal process or caudal protuberance of any kind.

TABLE FOR THE IDENTIFICATION OF LARVAE.

Hoplocampa halcyon Nort., *H. xantha* Roh. and *H. (MacGillvrayella) lacteipennis* Roh.

	H. lacteipennis	*H. halcyon*	*H. xantha*
First instar	Tergum ten black; black patch on anal prolegs; head width 0.22 mm.; length 1.3 to 1.86 mm.	Tergum ten and nine black; head width 0.25 mm.; length 1.4 to 3 mm.	Tergum ten and part of nine black; head width, 0.29 mm.; length 1.23 to 2 mm.
Second instar	Tergum ten and nine black; head width 0.39 mm.; length 1.88 to 3.35 mm.	Tergum, ten, nine and eight black; head width 0.4 mm.; length 3 to 5 mm.	Tergum ten, nine and part of eight black; head width 0.4 to 0.45 mm.; length 2 to 4 mm.
Third instar	Tergum ten and part nine of light yellow; head width 0.59 mm.; length 3.4 to 7.8 mm.	Tergum ten, nine, eight and part of seven black; head width 0.61 mm.; length 4 to 6 mm.	Tergum ten, nine and eight black; head width, 0.65 mm.; length 4 to 5 mm.
Fourth instar	Abdomen wholly white; head width 0.88 mm.; length 7.8 to 9 mm.	Tergum ten and nine spotted with black; head width 0.9 mm.; length 6 to 7.2 mm.	Tergum ten, nine and eight yellow spotted with black; head width, 0.9 mm.; length 5 to 7 mm.
Fifth instar	No fifth instar.	Tergum ten, nine and part of eight spotted lightly with black; head width 1.0 mm.; length 6.5 to 9 mm.	No fifth instar.
Food Plant	*Prunus virginiana*	*Amelanchier spicata*	*Prunus virginiana*
Larval Period at Aweme, Manitoba.	May 15 to July 31	May 15 to June 29	May 15 to June 25

Key to the Instars.

Hoplocampa halcyon Nort., *H. xantha* and *H. (MacGillvrayella) lacteipennis* Roh.

A. Tergum of abdominal segments solid black.
  B. Tergum of tenth segment only, black.
    C. Black on posterior part of anal prolegs. Borer in the fruit of *Prunus virginiana*...**1st instar of H. (MacGillvrayella) lacteipennis.**
    CC. No black on anal prolegs. Borer in fruit of *Prunus virginiana*, ...**1st instar of Hoplocampa xantha.**
  BB. Tergum of ninth and tenth segments black.
    C. Length 1.88 to 3.55 mm. Width of head 0.35 to 0.4 mm. Borer in fruit of *Prunus virginiana*,..... **2nd instar of H. (MacGillvrayella) lacteipennis.**
    CC. Length 1.2 to 2 mm. Width of head 0.25 to 0.3 mm.
      D. All of terga of segments nine and ten black. Borer in fruit of *Amelanchier spicata*,.....**1st instar of Hoplocampa halcyon.**
      DD. All of tergum of tenth segment black and only the posterior part of the ninth. Borer in the fruit of *Prunus virginiana*,..... .....**2nd instar of Hoplocampa xantha.**
  BBB. Tergum of eighth, ninth and tenth segments black.
    C. Black patch on the caudal aspect of anal prolegs. Length, 4 to 5 mm. Width of head, 0.6 to 0.7 mm. Borer in fruit of *Prunus virginiana*,.....**3rd instar of Hoplocampa xantha.**
    CC. No black on anal prolegs. Length usually less than 5 mm. Head not wider than 0.5 mm.
      D. All of terga eight, nine and ten black, sometimes a very small black spot on the mesodistal end of segment seven. Borer in the fruit of *Amelanchier spicata*,..**2nd instar of Hoplocampa halcyon.**
      DD. All of terga nine and ten and only part of eight black. Borer in fruit of *Prunus virginiana*,..**2nd instar of Hoplocampa xantha.**
  BBBB. Tergum of eighth, ninth, tenth and part of the seventh segments black. Borer in fruit of *Amelanchier spicata*,..... .....**3rd instar of Hoplocampa halcyon.**
AA. Tergum of terminal abdominal segment merely spotted with black, if at all.
  B. Terminal abdominal segments white. Width of head about 0.88 mm. Borer in fruit of *Prunus virginiana*,..... .....**4th instar of H. (MacGillvrayella) lacteipennis.**
  BB. Tergum of ninth and tenth segments light yellow (may be faded out in alcoholic specimens). Width of head, 0.6 mm. Borer in fruit of *Prunus virginiana*,...**3rd instar of H. (MacGillvrayella) lacteipennis.**
  BBB. Tergum of ninth and tenth segments spotted with black. Width of head about 0.8 mm. Borer in fruit of *Amelanchier spicata*,..... .....**4th instar of Hoplocampa halcyan**
  BBBB. Tergum of eighth, ninth and tenth segments spotted with black.
    C. Terga white with black spots and only part of the eighth spotted. Borer in fruit of *Amelanchier spicata*,..... .....**5th instar of Hoplocampa halcyon.**
    CC. Terga light yellow with black spots. All of the eighth spotted. Borer in the fruit of *Prunus virginiana*,..... .....**4th instar of Hoplocampa xantha.**

The writer would like to express his indebtedness to Dr. W. P. Hayes of the Department of Entomology, University of Illinois, under whom the work was done for many valuable suggestions and criticisms in preparing the manuscript.

REFERENCES.

(1). **Bird, R. D.** Scientific Agriculture. Vol. VI, No. 10, pp. 353-357. 1926.
(2). ————. Life History Notes on Two Species of Sawflies Injurious to the Fruit of the Choke Cherry. (Sc. Agric. In Press).
(3). **Rohwer, S. A.** Proc. Ent. Soc. Wash., Vol. 20, No. 8, pp. 161-173. 1918.
(4). **Yuasa, H.** Ill. Biol. Mon. Vol. VII, No. 4. 1922.

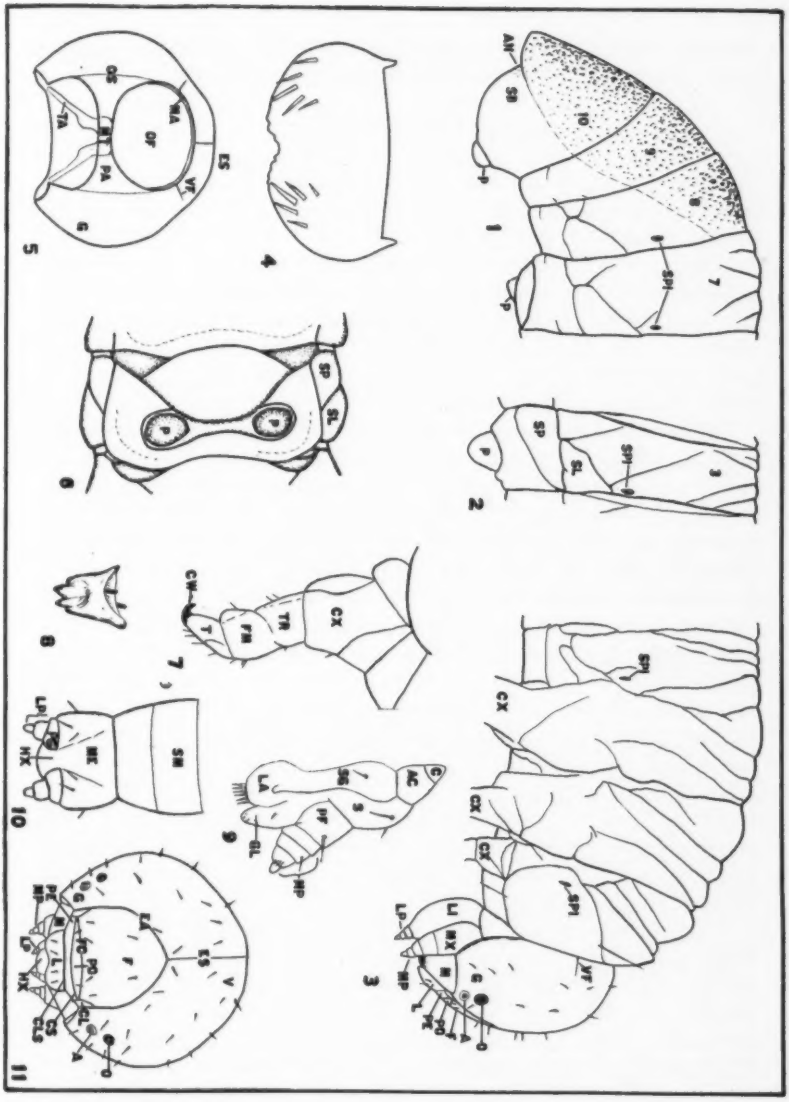
EXPLANATION OF PLATE XXIV.

The Larval Anatomy of *Hoplocampa halcyon* Nort.

Fig. 1. Lateral aspect of caudal abdominal segments. × 45.
Fig. 2. Lateral aspect of third abdominal segment. × 45.
Fig. 3. Lateral aspect of head and thorax. × 45.
Fig. 4. Epipharynx. × 160.
Fig. 5. Caudal aspect of head capsule. × 45.
Fig. 6. Ventral aspect of third abdominal segment. × 45.
Fig. 7. Caudal aspect of prothoracic leg. × 160.
Fig. 8. Mandible. × 160.
Fig. 9. Right maxilla. × 160.
Fig. 10. Labium. × 160.
Fig. 11. Cephalic aspect of head capsule. × 45.

LIST OF ABBREVIATIONS.

A.....antennaria.
AC.....alacardo.
AN.....anus.
C.....subcardo.
CL.....clypealia.
CLS.....clypeo-labral suture.
CS.....clypeal suture.
CW.....tarsal claw.
CX.....coxa.
EA.....epicranial arm.
ES.....epicranial stem.
F.....front.
FC.....fronto-clypeal suture.
FM.....femur.
G.....galea.
HX.....fused glossæ and paraglossæ.
L.....labrum.
La.....lacinia.
LI.....labium.
LP.....labial palp.
M.....mandible.
MA.....maxillariæ.
ME.....mentum.
MP.....maxillary palp.
MT.....body of tentorium.
MX.....maxilla.
O.....ocellus.
OF.....occipital foramen.
OS.....occipital suture.
P.....pseudopod.
PA.....postgena.
PE.....preclypeus.
PF.....palpifer.
PG.....palpiger.
PO.....postclypeus.
S.....stipes.
SB.....subanal lobe.
SG.....subgalea.
SL.....subspiracular lobe.
SP.....surpedal lobe.
SPI.....spiracle.
T.....tibia.
TA.....tentorial arm.
TR.....trochanter.
V.....vertex.
VF.....vertical furrow.


1
2
3
4
5
6
7
8
9
10
11
AN
SB
HD
T
A
SPI
SP
SL
CX
TR
FM
CW
LA
MP
MX
LP
SM
OC
VTA
PA
OF
ES
PE
PO
V

Ralph D. Bird

FURTHER STUDIES ON THE GENUS GYPONA AND IT'S ALLIES (RHYNCHOTA, HOMOPTERA).

By E. D. Ball and J. A. Reeves.

The systematic relations of this group were briefly discussed by the senior author in a previous paper.* It was recognized at the time as only a preliminary and tentative classification, hastily brought together and published in the hope of correcting a number of serious errors before they became established in the literature. During the past two years a number of the relatively rare species and varieties have been taken in numbers and food plants and life history observations on these and other species accumulated.

With the idea of more fully establishing the generic and specific limits in the group the junior author undertook to study the internal genitalia of all the available forms occurring in the United States. These studies not only confirmed the validity of the generic divisions established but definitely indicated that at least one more distinct generic group was advisable. The five divisions of the old genus *Gypona* all show distinct and strikingly different types of internal genitalia. *Dragonana* in many characters is more closely allied to *Xerophloea* than to *Gypona* proper and these two genera may well represent one line of development while the remaining genera represent another. *Dragonana* is either primitive or degenerate as judged by the simple internal genitalia. If we recognize irregularly recticulate venation as an indication of primitive character, as we probably must, then *Dragonana* may well represent the most primitive condition found in the group in our region, followed by *Gyponana*, *Gypona*, *Prairiana* and *Ponana* in the order named.

Gyponana rugosa is quite distinct in a number of characters from the other members of that genus and further study may warrant its segregation. Its internal genitalia are in certain characters very close to those of *Gypona glauca*, the type of the latter genus, and may indicate the line of divergence of the other groups from a primitive *Gyponana* type of ancestor.

*Ball, E. D. Annals Ent. Soc. Amer., Vol. XIII, p. 83-96, 1920.

The three species of *Prairiana* are strikingly distinct in their complicated pattern of internal genitalia and show closer affinities with *Ponana* than with *Gypona*. *Ponana resima* has been considered the extreme modification in this complex type, on the other hand it may represent a primitive type. An extended study of the South American forms will be necessary to determine this. The pygofers in this species carry a long curved spine, a character not observed in any other member of this group.

KEY TO THE N. A. GENERA OF GYPONINAE.*

A. Dorsal surface or at least elytra deeply pitted, body doubly wedge-shaped, elytra becoming vertical towards apex.
B. Pronotum pitted, front narrow, elongated, spines on hind tibia few, 1. **Xerophloea** Germ.
BB. Pronotum striate, front broader wedge-shaped, spines on hind tibia numerous, stout.....2. **Dragonana** Nov.
AA. Dorsal surface not pitted except possibly along veins, body elongate or oval, elytra not appressed at apex.
C. Elytra reticulate, or at least apically.....3. **Gyponana** Ball.
CC. Elytra with the venation regular or nearly so.
D. Face and vertex meeting in an acute angle, margin foliacious.
E. Elytra without markings in areoles, species green, golden or black.....4. **Gypona** Burm.
EE. Elytra with dots or lines in areoles, species straw or smoky, 5. **Prairiana** Ball.
DD. Vertex rounding to face or overhanging, rarely with a slightly produced thick margin.
F. Elongate, clypeus acute, elytra not overlapping..6. **Ponana** Ball.
FF. Oval, clypeus truncate, elytra broadly overlapping posteriorly, 7. **Penthimia** Germ.

Genus **Dragonana** nov.

Intermediate in form and structure between *Gyponana* and *Xerophloea* with the pronotum definitely broadened and almost angled posteriorly. This broadening serves as the base of a short blunt anterior triangle and also of a long acute posterior one. Head much narrower than body, vertex obtusely angular, lower than the plane of the pronotum, the anterior margin slightly foliaceous. Ocelli on the vertex about equidistant between the anterior and posterior margins and between themselves and the eyes. Front narrow, flat, slightly wedge shaped as in *Gyponana*. Pronotum transversely striated, convex in

*Fowler in the Biologia lists *Epiclines* A. and S. (from India) with a single (new) species from Mexico and Central America, but omits *Xerophloea*, which occurs throughout both North and South America. There is nothing in Fowler's figure or description that might not apply to a large species of *Xerophloea* and it has been thought best to omit *Epiclines* from consideration as a New World form until the generic relationships can be determined.

both diameters, the anterior submargin very much depressed, rounding in front, straight behind. Elytra long, relatively narrow, appressed posteriorly, becoming vertical at the tip. Whole surface closely pitted or ornamented with setigerous pustules. Venation weak and indefinite with some irregular reticulations in the forks and toward the apex. Whole surface milky subhyaline with dark setigerous punctures.

Type of Genus *Gypona dracontia* Gib. (Ariz.).

This genus is quite distinct structurally and probably represents a more primitive type than either *Gyponana* or *Xerophloea*. Superficially this species might be taken for a *Xerophloea* but the members of that genus have the head and pronotum pustulate instead of striate and the elytra have a definite cell pattern toward the apex.

Gyponana octolineata Say.

This is one of the most puzzling and variable forms in the whole group and has been the subject of much difference of opinion as to specific and varietal limits. It ranges from coast to coast and from Canada to Mexico and probably on to South America. It is the most abundant species in most of its range and varies from small pale forms of 9 or 10 mm. to the robust ones of 13 or 14 mm. in length. Certain forms are heavily and irregularly reticulate while in others the reticulations are reduced to a few extra ones in the apical and anteapical cells. The authors have studied external structures and internal genitalia throughout and have found no character that is not widely variable if the series studied is large enough.

The following varieties seem to be relatively constant. They are for the most part correlated with differences in food habits or life histories which probably explain the partial segregation.

KEY TO THE VARIETIES.

A. Scarlet, or at least stripes and reticulations scarlet..1. **octolineata** Say
AA. Green or green with yellow stripes on vertex and pronotum.
  B. Elytra heavily and irregularly reticulate, usually including all or part of clavus.....2. **cana** Burm.
  BB. Elytra not reticulate at base or on clavus, sometimes with only a very few reticulations.
    C. Species large, 10 mm. or over, the apical part of elytra reticulate; often either striped with yellow or pruinose.
      D. Green with or without yellow stripes.....3. **striata** Burm.
      DD. Pruinose.....4. **pruinosa** Spbg.
    CC. Smaller, narrower forms, green shining, found on pine..5. **tenella** Spbg.

Var. *octolineata* Say is the "pink katydid" expression of this species and probably does not represent a true variety in nature and yet certain puzzling variations need to be considered before uniting it with the second. It is found from Missouri and Minnesota eastward to the Atlantic, a region in which *striata* is the dominant form and yet the red *octolineata* forms are often heavily reticulated and apparently cannot be simply a red phase of the less reticulate variety.

Var. *cana* Burm. a short compact heavily reticulate form occurs in less numbers than *striata* from the Atlantic to the Pacific and from Canada to Mexico. It appears to be more abundant in the extreme southern region of the U. S. Nymphs and adults have been taken in numbers from the shrubby growths of the Florida flat woods. The nymphs are usually heavily dotted with brown and frequently margined with reddish brown. They are more abundant on *Pyrus* and *Vaccinium* than on the Myrtles. Burmeister describes this form as with an angulate vertex, but only an occasional example shows this character. He gives the length the same as that of *striata* but on the average *striata* will run a millimeter longer and all the extremely large examples seen have been of that form.

Var. *striata* Burm. is the commonest form found on the Pacific Coast and as stated above the dominant one in the Northern U. S. and Canada. The largest forms found in the United States (often as much as 13–14 mm. in length) are found here. The nymphs are found in almost all situations where mixed vegetation, weeds and shrubs occur. These are rare in pure grass stands or on isolated trees or pure tree stands. The true character of *G. quebecensis* Prov. has been a puzzle. Van Duzee insists that it is distinct, and characterizes it as small and heavily reticulate, although after he examined the Provancher collection in the museum at Quebec he recorded the specimen found there as a typical *cana*. Osborn in his Leafhoppers of Maine describes a small (8–9 mm.) slightly reticulate form as *cana* and lists *quebecensis* as a synonym, but Van Duzee in his catalogue places this reference under *quebecensis* despite the sparse reticulations. There appears to be no reason to believe that *quebecensis* is other than a synonym of *striata*, the common form in the region where Provancher worked. He recognized and described two species and only two, *quebecensis* = *striata* and *hullensis* = *pectoralis*, the two common forms found there.

He says nothing about reticulations, but gives the length as longer than *pectoralis* and its occurence as in damp places which would be correct for *striata*, but would not fit in with the idea of a small species, such as Van Duzee and Osborn describe or with *tenella*, the only small form occurring in that region that we have been able to differentiate.

Var. *pruinosa* Spgb. Spangberg described this form from Georgia and Texas placing it between *flavolineata* and *scrupulosa*, both forms of *striata* without giving any character by which it could be separated except the name. Certain pruinose forms from that region resembling *striata* have been placed here, but at the best it is a weak variety and pruinose forms also occur in *tenella*. The size given and the location in his system both incline one to believe that this is a pruinose variety of the larger forms.

Var. *tenella* Spgb. (*Gypona geminata* Osb. *Gypona quebecensis* Van Duzee, and Osb. in part (not Prov.). This is a small (7–9 mm.) pale green, almost parallel margined variety with relatively few reticulations; in some of the smaller examples they are almost absent. Some of the Northern examples have relatively strong reticulations in the anteapical and apical regions and may be what Van Duzee had in mind as *quebecensis* and what Osborn referred to in his Maine list. Provancher, however, described a larger insect, as noted under *striata*.

Osborn records it from pine on Long Island. Examples are at hand from Cranberry Lake, N. Y. (Osb. and Drk.). The senior author has taken it from Jack Pine in Northern Wisconsin, in August, and the writers have taken it commonly from Long-Leaf Pine in a number of places in Florida during the past two years.

The usually smaller size and shorter head, as well as its association with pine, would seem to warrant specific rank, but a study of internal as well as external genitalia of numerous examples from Florida and Wisconsin compared with a long series of *striata* and *cana* from Florida, District of Columbia, Wisconsin, Iowa, Colorado, Utah and California shows no more than individual variation throughout the series.

Examples of a pruinose form of this species from Southern Florida, also taken on pine, and an example from Costa Rico extend the distribution and suggest further synonymic complications when the Mexican and South American tangle is worked out.

It was through a misinterpretation of Spangberg's comparison of this species with *bigemmis* that it was placed as a synonym of *angulata*. The smaller size (7–8 mm.), round head and pale color described all fit this form much better than any other occurring in the Georgia region.

Gyponana rugosa Spgb.

Specimens of this species are at hand from Boston, Mass., District of Columbia, Virginia, Wisconsin, Southern Colorado, and Salt Lake, Utah, all collected by the senior author from oak; specimens have been examined from Texas, New Mexico and several places in Arizona and Costa Rico. The writers have found nymphs and adults on nearly all species of oaks in Florida. It is apparently, only limited in distribution by the range of its food plant, the oaks.

The species, while heavily reticulated, is quite distinct in the genus *Gyponana* and in other characters is very close to *unicolor* and its relatives in *Gypona*. The nymphs are thickly covered with long silky hairs, while the nymphs of other species have relatively inconspicuous ones.

Gyponana chadana nov. sp.

Similar to *rugosa*, but smaller with narrower head and a long and acutely angled vertex. Length, 8 mm.

Head much narrower than pronotum, vertex almost as long as pronotum, right angled, with the margin very slightly convex; ocelli almost equidistant between base and apex, set well in front of eyes, equidistant from each other and the line of the eyes; front narrow, inflated so as to appear straight to the apex of the vertex in profile. Pronotum broad and short, rapidly narrowing from the prominent lateral angles to the very small eyes; elytra resembling *rugosa* in the type and pattern of reticulation, but narrowing posteriorly and lacking an appendix.

Color pale golden as in *rugosa* (greenish in life) but lacking the stripes of that species except a pair on scutellum. A pair of black spots on pronotum, another on hinges and milky white markings between the reticulations as in *rugosa*.

Holotype male, "Chads," Utah, July 11, 1910 (Ball). Swept from oak (*Q. undulata* var. *wrighti*.). This is a strikingly distinct addition to this group. In head character it resembles *angulata*, but is much narrower and even more acutely angled, while in other characters it is close to *rugosa*, but again narrower and more acute at the apex of elytra.

Gypona signoreti Stal.

This species varies from golden green to tawny or even reddish with a smoky cloud in the apical cells. The females are about the size and shape of the western males of *unicolor*, but with a shorter and less foliaceous vertex. This species was described from Mexico and the female examples are at hand from Salt Lake, Utah in August, and Cedar City, Utah in September taken on oak (Ball):

Var. *pilula* nov. Intermediate in form and color between *tenella* and *signoreti*. Smaller than *tenella* (7 mm.) golden or bright straw (green in life), with red eyes and ocelli, vertex quite definitely but slightly obtusely angulate, front slightly inflated so as to almost eliminate the foliaceous margin, female segment truncate, veination as in *unicolor*.

Holotype female, Allotype male and four Paratypes collected by Ball at "Chads," Utah, July 11, 1910, on *Cowania mexicana*. The material reported as *unicolor* by Ball from Arizona and that collected on oak at Dolores, Colo., (Aug., 2, 1900) belongs to this variety. A nearly full grown nymph was taken with the types. *G. signoreti* appears to be widely distributed through Mexico, the West Indies and on to South America and no doubt there will be some synonomy and many of its varieties will have been named, but most of its variations in the humid tropics are towards the reds with dark margins, while this form from the extremely arid dwarf oak environment, is strikingly small and pale.

Gypona unicolor Stal.

Gypona melanota Spgb., *G. bipunctulata* Wood., *G. nigra* Woodw., *G. germari* Fowl. (not Stal).

This large, broad, green, species with five varieties of males ranging from pure green to shining black is now known from Massachuesetts to Utah and south to Georgia in the Alleghanies and to Panama in the mountain meadows of the Rockies. The senior author has collected it in District of Columbia, Virginia, Wisconsin, Minnesota, Iowa, North Dakota, Colorado and Utah, and has examples from New York, West Virginia, Kansas, Sierra Madre Mountains and Nepantla, Mexico. Spangberg described it from New Jersey and Georgia, Fowler (as *germari*) lists it for Mexico and Central America. It has not been taken in Florida or in the southern Mississippi valley

and will probably be found to be confined to the northern prairie belt with extensions southward in the mountains. The Colorado and Utah examples were found in high mountain meadows with heavy grass covers. The western material is all relatively longer and narrower than that from the humid east.

This species was listed as *melanota* Spgb. in the former review, as at that time no material had been studied (the western material was as yet unmounted) from the Rocky Mountain region or southward and all descriptions from this region were thought to apply to the following species. On restudying these descriptions with the new material it became fairly certain that *unicolor* of Stal. was based on a female of this species without spots on the pronotum and that the species listed by Fowler as *germari* was *unicolor* and not *angulata* as formerly suggested.

Gypona verticalis Stal.

Material of this species is at hand from many places in Colorado and Utah (Ball) New Mexico (Townsend), Arizona (Williams) and from a number of places in Mexico. The synonomy given before appears to be correct and in addition it is probable that *fuscinervis* Stal, which was described from a single male, will be found to belong to this group, in which case the name will take precedence. This species is found in the clumps of Snowberry growing on rocky ridges and warm mountain slopes and is typically arid in its distribution, while on the other hand *unicolor* is found only in the high wet mountain valleys in the arid regions and is typically humid in distribution.

Prairiana cinerea Uhl.

This rusty straw-colored species in its many striking varieties ranges from Massachusetts to California and from Montana to Mexico, but is abundant only in the short grass region and the transition zone to the prairies. Isolated examples have been found in Iowa, Illinois and Connecticut on the east and in extreme southern California and down to Vera Cruz, Mexico on the west. Ball suggested that the Massachusetts reference probably belonged to *miliaris*, but through the kindness of Dr. DeLong, the writers have examined a typical example of var. *kansana* from Connecticut (Garman). The senior author in many years collecting west of the Rocky Mountains only found

it in one isolated spot in Southern California. Varieties *kansana* and *subta*, two of the extremes, were the only ones with sufficient material for study, but there was no appreciable difference in their internal genitalia.

P. cinerea var. *moneta* Van D., resembles *kansana*, but is much smaller, narrower, with a long and extremely foliaceous vertex, smoky with the vertex and pronotum paler. This variety seems to be confined to the extreme Southwest. It was described from three females from the Gulf of California and the senior author took two males at Chino, California, in June.

P. cinerea var. *orizaba* nov. var. Still longer and more slender than *moneta*, as long as *kansana*, but much narrower, pale straw with a few elongate dashes around the margins of elytra. Length, 9 mm.

Vertex and pronotum much elongated, over three-fourths of vertex in front of eyes, acutely subangular with the apex rounded. Elytra very long and narrow, pale straw. The vertex and pronotum very finely irrorate with scarlet, a pair of fine fuscous points back of the ocelli and a few irregular linear dashes in the areoles mostly around the margins.

Holotype male Orizaba, Mexico, January 9 to 16, '92 (H. Osborn). Type in senior authors collection. This must also, be a rare form as it does not seem to be listed in the Biologia.

Genus **Ponana** Ball.

This genus is distinctly subtropical in distribution only one species (*scarlatina*) occurring in the Northern States and then with only 3 or 4 of its numerous varieties. The past two years collecting in Florida has brought together a large amount of material in this group. The internal genitalia of all these forms has been studied and as a result several more forms previously recognized as distinct species have been found to be only varieties of *scarlatina*. On the other hand the new materials has indicated that several more varieties are sufficiently constant and have food plant or environmental factors that warrant their recognition.

KEY TO SPECIES OF PONANA.

A. Vertex moderately long and slightly produced, elytra usually with spots, dots or flecks.
  B. Vertex longer, species variable in color, moderate to large, 1. **scarlatina** Fh.
  BB. Vertex shorter, species small dull gray.....2. **curiata** Gib.
AA. Vertex short and very broad, almost parallel-margined elytra with apical and discal cells free from spots or dots.
  C. Pale green with concolorous nervures, often with black along suture, vertex margin thick but definitely produced...3. **dorsalis** Spbg.

CC. Brown with darker nervures, vertex margins rounding broadly to face, ocelli just back of margin.
D. Nervures lightly, narrowly lined with brown, spots along anterior margin of pronotum.....4. **marginifrons** Fowl.
DD. Nervures brown, marginal spots on pronotum back of eyes only. 5. **resima** Fowl.

Ponana scarlatina Fitch.

There are a number of additions to the former list of varieties and some consequent regrouping as shown in the following key.

KEY TO THE VARIETIES.

A. Smoky or pale with little trace of red (rare in **puncticollis**), areoles without red flecks and rarely with a few transverse vermiculations.
B. A smoky median stripe or heavy transverse fuscous vermiculations, without pronotal spots (at most 2). (Northern varieties).
C. A variable smoky brown median line, few if any transverse vermiculations.
D. Elytra smoky with only lateral margins pale..1. **limbatipennis** Spbg.
DD. Elytra with only a narrow median line smoky....2. **pectoralis** Spbg.
CC. No smoky median line, heavy transverse vermiculate reticulations, 3. **scarlatina** Fh.
BB. Pale varieties usually with four spots on submargin of pronotum and four on each elytron, two large on claval suture and two smaller on margin in form of pack saddle (mostly Gulf Coast).
E. Pale brown or with a reddish tinge, spots on pronotum and elytra and some transverse vermiculate lines at least along suture.....4. **puncticollis** Spbg.
EE. Yellowish or greenish varieties, sometimes almost white, no transverse vermiculate lines, pack saddle spots on elytra.
F. Stout, yellowish, no spots on pronotum.....5. **citrina** Spbg.
FF. Smaller, more slender greenish four spots on pronotum, 6. **meditabunda** Spbg.
AA. Red or red flecked or brownish, with numerous definite dots or spots in the areoles.
G. Elytra without black spots in the areoles, except for the pack saddle and a few other paired marks, whole insect usually flecked.
H. Scarlet or testaceous varieties.
I. Heavily flecked with scarlet, the nervures inconspicuous, 7. **irrorella** Spbg.
II. Testaceous, the nervures conspicuous, red flecking faint or absent.....8. **rodora** Ball.
HH. Straw colored with faint red flecking giving a reddish tinge, pack saddle marks, the base of appendix and one or two pairs of spots adjoining dark.....9. **pauperata** Spbg.
GG. Elytra with numerous black spots in the areoles, a pair of black spots on the pronotum back of ocelli, rarely more than a trace of red flecking.
J. Ground color scarlet by virtue of inconspicuous red flecking, 10. **sanguinolenta** Spbg.
JJ. Ground color dirty straw, washed with pale brown.
K. Spots in areoles inclined to be round and irregularly placed, a single pair of black spots on pronotum back of ocelli, 11. **grisea** Spgb.
KK. Spots in areoles inclined to be transverse and arranged along nervures, usually a pair of spots on base of vertex, another on pronotum in line with ocelli and two additional pairs, forming a crescent.....12. **dohrni** Stal.

The food plants and habitats of the varieties are quite strikingly diverse and suggest that there are at least three groups of species involved. The study of both external and internal genitalia from long series of examples, however, gives no basis of separation and each locality seems to have its own slight variation from the type as well as extremes that intergrade in all directions.

Var. *limbatipennis* has been recorded from Buttercups and *pectoralis*, from Basswood, *scarlatina* has no recorded food plant but has been taken where Basswood and Buttercups were both abundant.

Var. *puncticollis* both nymphs and adults have been taken from Basswood sprouts in deep shady swamp areas in Florida the past year.

Var. *citrina* occurs abundantly in damp shaded areas where the Labiate *Micromeria brownei* forms dense mats. The green nymphs and greenish creamy adults have both been taken from these mats.

Var. *meditabunda* has been taken in low flat pine woods, usually in open grass and swampy areas where the little water pennywort (*Hydrocotila*) is abundant.

Varieties *irrorella*, *rodora* and *pauperata* are all very strictly confined to the mat like areas of the Gopher plum (*Chrysobolanus oblongifolius*) occurring in the high, dry, sandy areas. The difference in color and markings is largely a seasonal effect. The brilliant red flecked *irrorella* is largely a summer form, the dark coppery *rodora* a summer and fall extreme while the pale *pauperata* is the winter and spring form. The nymphs of all these forms are dark red. *G. spadix* DeLong, proved to belong to var. *rodora* on examination of an example kindly sent by Dr. DeLong.

Var. *sanguinolenta* is found both larvæ and adults in the thick mats of the low growing oaks in the higher spots of the flat pine areas.

Var. *grisea* also appears to feed on the low oaks but only where they are in deep shade of the hammock forest type probably a different species of oak as the relative abundance of the species of low oaks is quite different in the two areas.

Var. *limonea* nov. Form and size of *pectoralis*, but entirely lacking the dark markings. Uniform pale tawny yellow, glistening, the eyes and ocelli dark brown, disc of scutellum paler.

Holotype female and paratype female, Vinton, Ohio, June 5, 1900 (Osborn Collection).

Allotype male and paratype female, Washington, D. C. (Ball Collection).

After the completion of this paper Doctor Osborn sent a large tawny yellow female that at first sight was mistaken for *Gypona unicolor*, but on examining the vertex margin it proved to be a *Ponona* and evidently the pale extreme in the *limbati-pennis-pectoralis* group. The more tawny examples of *citrina* are similar in color, but the thickening of the apex of the head will at once separate them.

Ponana resima Fowl.

This species occurs abundantly on the mat forming oaks and both nymphs and adults are occasionally found on practically all species of oak. The nymph is easily recognized by its blunt head, alternate red and green bands and the presence of silver scales on the dorsum.

The Nymphs

The generic characters in the nymphs are as definite and constant as those in the adults, *Xerophloea* nymphs have an even larger and more foliaceous, angularly pointed, head than the adults and a similarly tapering body. *Gyponana* nymphs are green, flat with long foliaceous vertices that are definitely narrowed immediately in front of the eyes. The antennæ are extremely long and thread-like. *Gypona* nymphs are heavy bodied with long vertices that are thickened slightly at the apex. The antennæ are shorter and the bristles on the body sparse but strong. *Prairiana* nymphs are dirty rusty straw colored usually dotted with black. They are almost parallel margined with very long foliaceous heads. The eyes are very small and set into the posterior part of the margin. The front is very long and narrow, the antennæ short and the first three segments large. *Ponana* nymphs are red or reddish green, short and stout bodied with relatively short rounding vertices. The front is broad, the antennæ short and the hind legs extremely broad and bowed. *Penthimia* nymphs are red and even shorter and rounder than those of *Ponana* with heavily overhanging vertex margins. The abdomen is shorter than the thorax.

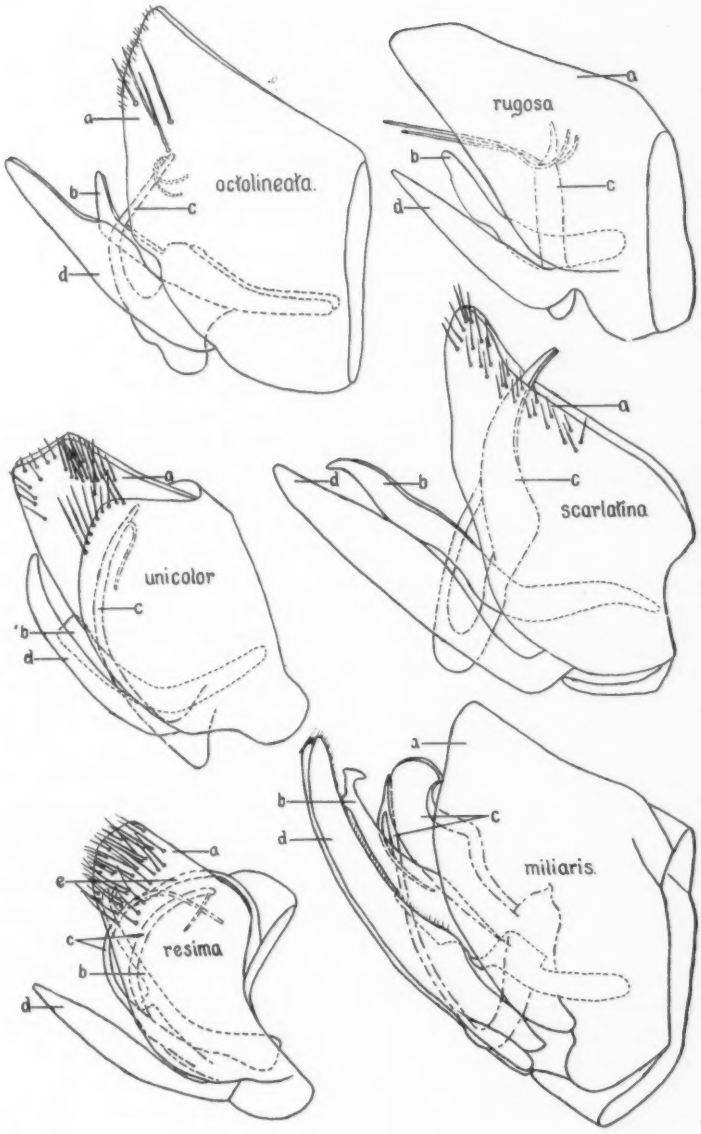
EXPLANATION OF PLATES.

PLATE XXV.

Internal Genitalia of typical species of each genus in situ. a, Pygofer; b, Styles; c, Oedagus, d, Plates; e, Pygofer spine.

PLATE XXVI.

Showing style and oedagus of each species arranged by genera. The style is on the left and the oedagus on the right. The oedagi except in *rugosa* and *angulata* viewed from the side. All drawings made to the same scale from cleared and dissected material in permanent balsam mounts with the cover glass pressed down.



Ball and Reeves.

Ball and Reeves

THE APPLICATION OF STUDIES IN HYDROGEN ION CONCENTRATION TO ENTOMOLOGICAL RESEARCH.

By DAVID E. FINK, Ph. D.

Associate Entomologist, Truck Crop Insect Investigations, Bureau of Entomology, United States Department of Agriculture.

INTRODUCTION.

In all living matter biochemical reactions within and without the cell are continually influenced by hydrogen and hydroxyl ions which have, therefore an important significance in all biological studies. Although this phase of investigation upon insects has hitherto received little attention, there are many problems in which a knowledge of the concentration of these ions is of significance in entomological research. A few typical examples may be cited to indicate the relationship.

Many injurious species of insects of economic importance pass at least part of their development in a soil medium, the pH of which plays an important role in development of the insect and incidentally in control. The application of studies in hydrogen ions to life-history work in general will lead to a greater insight into the process of growth and development. Moreover, a better understanding of host preferences may be gleaned as a result of studies of the pH of the body fluids of insects and of the host plants upon which they feed. Of paramount importance in preventing injury to susceptible plants is a knowledge of the pH of arsenicals and other substances used as sprays. In studying the effect of arsenicals or other substances upon insects, the control of the pH of dilutions used in the experiments is essential in order to eliminate the influence which the H or OH ions may have upon insects. Studies on digestion and nutrition require a knowledge of the pH of the alimentary tract. In all biological work problems constantly arise that invlove a knowledge of the absolute effects of these ions as they exist in various solutions.

It is quite evident from the few examples cited that studies in hydrogen ion concentration should become part of many biological investigations in entomological research.

Methods for Determining Hydrogen ion Concentration in Small Quantities of Fluid.

THE INDICATOR METHOD.

Unfortunately the quantity of fluid available for study in single insects is usually of the magnitude of about 0.01 cc, equivalent to a medium-size drop, though in certain stages of insects, as the larvæ of most species and in the adults of certain *Orthoptera* and *Coleoptera*, it may be possible to obtain several drops of fluid. On the other hand it is quite impossible to obtain even a drop of fluid from the adults of most *Lepidoptera*, *Diptera*, and *Hymenoptera*.

With so little fluid available it has, hitherto, been out of the question to utilize the potentiometer method for pH measurements, and several investigators when dealing with minute amounts of fluid have utilized the indicator method described by Felton (3) and others. This method has been found very convenient by the writer for obtaining approximate results, and in principle consists in comparing the color produced by an unknown drop of fluid to the colors in a series of known drops of buffer solutions having definite pH values to which a drop of some indicator had been added. The accuracy of this method is within 0.1 to 0.2 pH, which for ordinary purposes is quite sufficient.

The equipment necessary for the indicator method is very inexpensive and consists of the following: (1) an opal glass plate, (2) a set of standard buffer solutions, (3) a set of indicators, (4) several stirring glass rods. These may be obtained from any chemical firm. Buffer solutions may be purchased in definite pH units or as a Universal Buffer Solution and dilutions made up according to the series of pH units desired. The writer found the latter method expedient and more desirable, since if by chance a buffer solution should become contaminated or if additional units were needed during the progress of some investigation these could be made without loss of time. If the latter method is adopted it is essential that the buffer solutions be placed in 30 cc. stock bottles fitted either with ground-glass pipettes or with Barnes pipette stoppers. This equipment insures a pipette with each buffer solution delivering drops of equal volume. The indicator solution should be

stored in similar type bottles to deliver uniform drops. The indicators recommended by Clark (1) and Clark and Lubs (2) can be purchased as powdered dyes and the solutions made according to the directions given by the above authors, or the indicators may be purchased in solution ready for use. The following indicators were found useful in ordinary work encountered in entomological research: Brom cresol green (pH4—5.6), brom cresol purple (pH 5.2—6.8), brom thymol blue (pH 6.0—7.6), and phenol red (pH 6.8—8.4).

Method of Procedure.

The procedure in determining the pH of an unknown solution is as follows: A series of drops from standard buffer solutions having a wide range of pH, as, for example pH 4, 5, 6, 6.8, 7 and 8, are placed upon an opal glass plate, and to each of these is added a drop of indicator having the same range of pH as the buffer solution, and the drops are mixed by means of the glass rods. A series of drops of the unknown are similarly arranged in a row, each receiving a drop from a different indicator, and mixed by means of the glass rods. The resulting color of the unknown is then matched against the colors produced by the known buffer solutions. This procedure serves as a "feeler" for determining the approximate pH of the unknown. The next step is to make a closer and more accurate determination of the pH of the unknown by comparing to buffers in units of 0.1 pH. After several trials in comparing colors it becomes comparatively a simple procedure to determine the pH of the unknown.

The simplicity of the indicator method favors its adoption as a field method for entomological work of the kind outlined above. Unfortunately the blood of many species of insects is highly pigmented and the color in many instances interferes with the pH determinations by the indicator method. Felton, however, recommends the use of stronger indicator solutions when dealing with colored or turbid fluids. This may be of advantage for certain types of work. If, however, difficulty is experienced in obtaining consistent results, resort must be had to the potentiometer method.

Ordinary sanitary precautions are to be observed when dealing with the indicator method. The drops of fluid for comparison should be of the same volume, and the glass rods

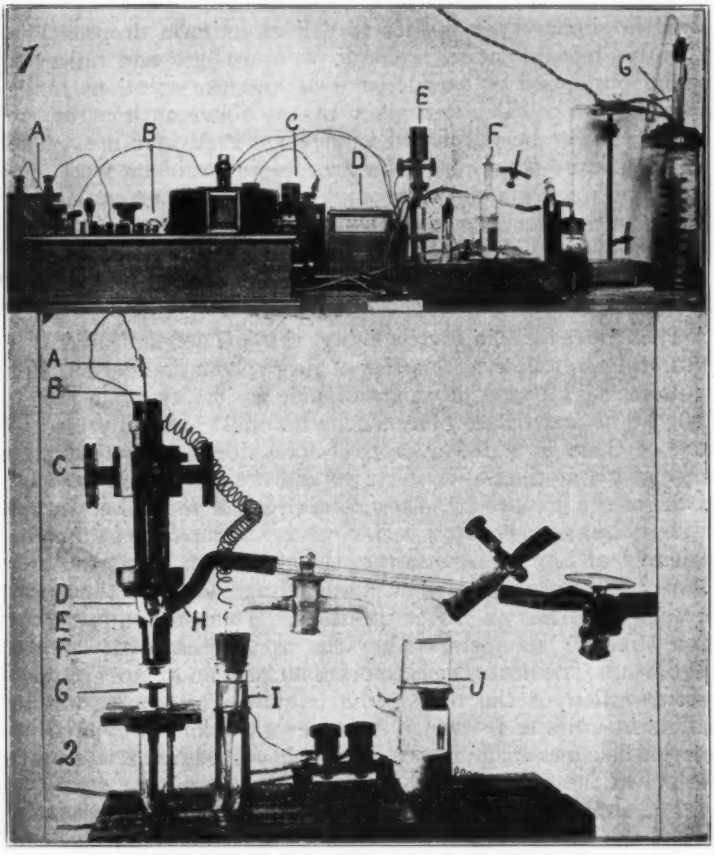


FIGURE I

(1.) Assemblage of apparatus for the electrolytic determination of the pH of the blood of insects. A, standard cell; B, potentiometer; C, 4-volt battery furnishing the E. M. F.; D, galvanometer; E, modified microscope in which is mounted the electrode vessel containing the platinum electrode; F, the calomel electrode; G, the hydrogen generator.

(2.) Electrode vessel mounted on a modified microscope and calomel electrode connecting with the KCL solution in the U tube, all mounted on a wooden base. A, copper wire connecting by mercury with electrode; B, capillary glass tube holding the platinum electrode; C, coarse adjustment for lowering or raising the electrode vessel; D, the glass vessel; E, platinum electrode; F, capillary tube for testing fluid; G, U-tube of saturated KCL bridge; H, arm fused on side for hydrogen intake; I, arm for calomel electrode connecting with the KCL bridge; J, calomel electrode.

used for mixing the solutions should be cleaned to prevent contamination of one solution with another. It is also necessary to make the determinations very quickly to minimize exposure of the unknown to the influence of the carbon dioxide of the air, as the exchange of gases takes place rapidly on exposed surfaces.

THE POTENTIOMETER METHOD.

The large number of books published on the subject of hydrogen ion concentration and the many bulletins issued by makers of potentiometer apparatus explain this method in detail. It will be necessary, therefore, only to point out the improved hydrogen electrode vessel described by Bodine and Fink (4) for the purpose of making the potentiometer available for the pH determination of minute amounts of fluids.

The entire apparatus assembled for the purpose of hydrogen ion measurements is shown in Figure I (1) and consists of potentiometer, standard cell, 4-volt battery, box galvanometer, dry cells, hydrogen generator, and the modified hydrogen electrode vessel mounted in the tube of a modified miscroscope with the calomel electrode and KCL bridge all held rigidly in a small wooden base. An enlargement of the hydrogen electrode vessel and calomel electrode mounted on the wooden base is shown in Figure I (2). The electrode vessel is shown mounted in a modified tube of the microscope, the capillary part of the vessel contains the fluid to be measured and by means of rack and pinion the entire vessel with capillary may be lowered into the saturated KCL solution in one arm of the U tube. An extension from the calomel electrode fits into the other arm of the U tube. Passing through the hydrogen electrode vessel is a capillary glass tube with sealed platinum wire—the platinum electrode. This tube is filled with mercury. Both the hydrogen electrode vessel and platinum electrode are so adjusted that the platinum point is exactly centered and can be raised or lowered, making contact with the surface of the fluid in the capillary. Wires from both the calomel and platinum electrodes lead to the potentiometer and the potential difference of the fluid in the capillary portion of the vessel is read in millivolts on the potentiometer and calculated in pH values.

To determine the hydrogen ion concentration of the body fluid of an insect, for example, a puncture is made mid-laterally

by means of a needle and the drop of fluid that oozes out is held against the tip of the capillary and sufficient fluid is drawn up to fill the capillary. In some species by cutting off a leg or a wing sufficient fluid is obtained to fill the capillary. By means of the platinum electrode that passes through the electrode vessel, contact with the surface of the fluid in the capillary is made; and by means of rack and pinion the electrode vessel is lowered and contact established with the KCL solution in the U tube. These contacts close the circuit of the system, and the potential difference of the fluid is read on the potentiometer. Of course, previous to determining the pH of any unknown fluid, it is essential to have the potentiometer in perfect balance with the standard cell, and to check the platinum electrode with a standard buffer solution.

After each reading, the fluid in the capillary is drawn off by means of filter paper held against the tip of the capillary which is afterwards flushed several times with distilled water and hydrogen. Between readings it is advisable to use some standard buffer solution in the capillary to test the sensitivity and accuracy of the platinum electrode.

Precautionary Measures.

Several precautionary measures are to be considered to avoid difficulties in manipulation and to obtain consistent results. The platinizing of the platinum electrode should be prepared as explained by Michaelis (5) and when not in use this should be kept in pure water. The electrode vessel should receive a steady flow of pure hydrogen from the generator to maintain a definite positive pressure, and prevent diffusion of fluid from the saturated KCL solution. If difficulty is experienced in obtaining a perfect balance with the standard cell, the battery furnishing the E. M. F. probably needs recharging. The platinum electrode should be perfectly centered and not touch the sides of the electrode glass vessel, otherwise readings will vary and a lag follow. In cleaning and dislodging bubbles of air in the capillary, the use of a fine wire will be found useful. For other precautions see Clark (1), and Bodine and Fink (4).

Experimental Results.

From the many problems in hydrogen ion concentration outlined previously that need to be investigated, an attempt has been made, first, to determine the reactions of the body fluids in a large number of species of insects belonging to several orders; secondly, to determine the relative changes, if any, in the hydrogen ion concentration that may occur during

Table I. The pH of the Blood of Insects Belonging to Three Orders.

Species	Average pH
Lepidoptera. Average pH 6.53.	
Pieris rapæ L.	6.64
Autographa brassicæ Riley	6.55
Malacosoma americana Fab.	6.50
Heliothis obsoleta Fab.	6.56
Datana ministra Dru.	6.35
Agrotis ypsilon Rott.	6.60
Coleoptera. Average pH 6.85.	
Cotinis nitida L.	7.14
Popillia japonica Newm.	6.85
Pheletes agonus Say	6.91
Leptinotarsa decemlineata Say	6.62
Harpalus caliginosus Fab.	6.89
Harpalus pennsylvanicus DeGeer	6.90
Tenebrio molitor L.	7.00
Diabrotica 12-punctata Fab.	6.50
Orthoptera. Average pH 7.10.	
Melanoplus femur-rubrum De Geer	7.02
Melanoplus differentialis Thos.	7.11
Dissosteira carolina L.	7.25
Microcentrum retinerve Burm.	7.07
Gryllus luctuosus Serv.	6.94
Concephalus brevipennis Scudd.	7.15

development of an insect from the egg to the adult form. All the pH measurements recorded in this paper were made by means of the potentiometer.

Data for the first problem were obtained upon a large number of individuals belonging to a species and the results averaged as shown in Table 1. In general there are slight differences in hydrogen ion concentration between species, but the general average for an Order gives results that indicate that the hydrogen ion concentration of species belonging to *Lepidoptera* is higher than for the species belonging to the

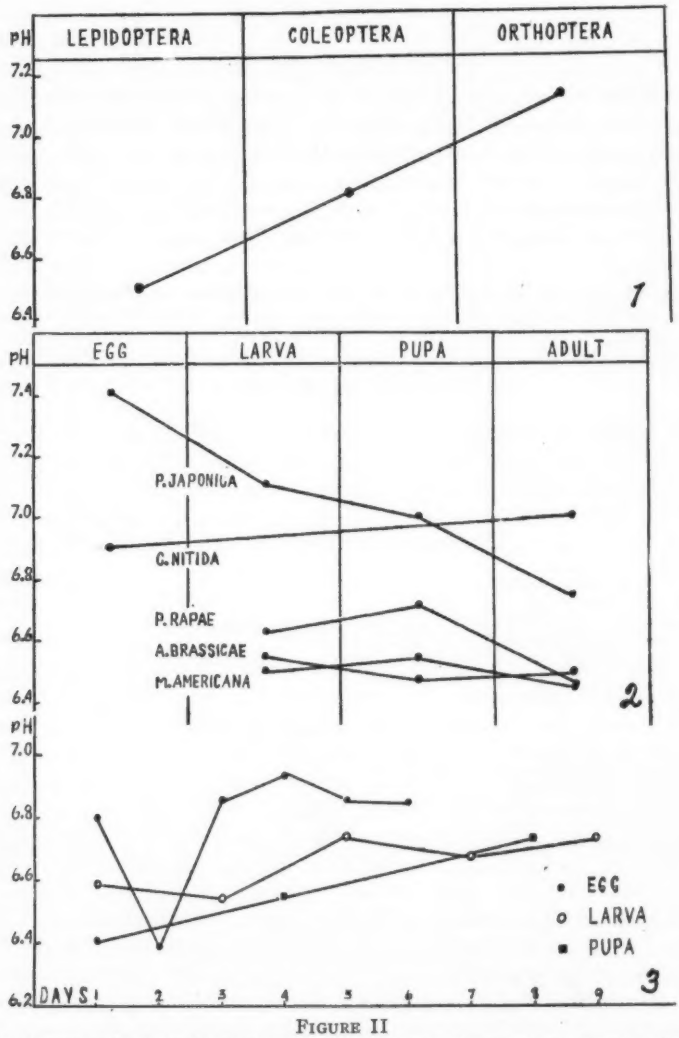


FIGURE II

(1.) Average pH of the blood of species belonging to three orders. Species of the order Lepidoptera indicate a higher hydrogen ion concentration than the species belonging to the orders *Coleoptera* or *Orthoptera.*

(2.) Average pH of the blood of various stages of species belonging to the orders *Lepidoptera* and *Coleoptera.* This figure shows that in nearly every stage of development of *Lepidoptera* the hydrogen ion concentration is greater than is the case with species belonging to the order *Coleoptera.*

(3.) Changes in pH that occur during development of the potato beetle (*Leptinotarsa decemlineata*) from the egg to the adult. Each point is the average of many determinations.

Order of *Coleoptera* or that of *Orthoptera*. From the results indicated graphically in Figure II (1–2) it is quite evident that this relationship seems to hold even for different stages of the species; that is, an acid medium for species belonging to the Order *Lepidoptera*, a less acid medium for species belonging to the Order *Coleoptera;* and a neutral medium or slightly alkaline for species belonging to the Order *Orthoptera*. Whether such a relation will continue to be maintained when data for a large number of species belonging to many Orders will become available, remains to be determined.

For the second problem the change in hydrogen ion concentration that may take place during development of an

TABLE 2. THE PH OF THE BLOOD OF THE POTATO BEETLE (LEPTINOTARSA DECEMLINEATA) DURING DEVELOPMENT.

EGG		LARVA		PUPA	
Days	Aver. pH	Days	Aver. pH	Days	Aver. pH
1	6.79	1	6.58	1	6.42
2	6.36	3	6.52	4	6.59
3	6.85	5	6.74	8	6.72
4	6.95	7	6.64		
5	6.82	9	6.71		
6	6.95				

insect from the egg to the adult was determined on the potato beetle, *Leptinotarsa decemlineata* Say. The method adopted was to obtain daily pH determinations on a large number of eggs from the time they were first deposited until they hatched. Measurements of the pH of the body fluids of larvæ were made upon a large number of individuals representing each stage of growth. Determinations of the pH of the body fluids of pupæ were made upon a large number of individuals on the first, fourth, and last days of development. The results have been averaged and are indicated in Table 2 and plotted in Figure II (3).

From this figure it is observed that although the initial pH of the egg on the first day is 6.79, it becomes on the second day more concentrated in hydrogen ions (pH 6.36) and in subsequent days the hydrogen ion concentration becomes less. Concerning the higher concentration of hydrogen ions that occur on the second day, one explanation might be the well

known fact that in its earlier stages the egg consists almost entirely of yolk. The splitting and breaking down of this fat material into fatty acids produce an acid medium. Whether in the upbuilding of the embryo the energy liberated in the breaking down process is utilized, is not known.

There appear but slight changes in the hydrogen ion concentration during larval development; first, second, third, and fourth larval stages give an average pH of 6.58; 6.52; 6.74; and 6.64, respectively, and the average pH of the body fluids of the larvæ as they enter the ground before pupation is 6.71.

Changes in hydrogen ion concentration of pupæ are rather more marked as indicated in Table 2 and Figure II (3). Furthermore, there is a well marked difference between the pH of the larvæ as they enter the ground for the purpose of pupation (pH–6.71) and that of the pupæ that are first formed (pH 6.42). As pupal development continues, however, the hydrogen ions become less concentrated until at the termination of pupal development a pH of 6.72 is obtained.

LITERATURE CITED.

1. **Clark, W. M.** The Determination of Hydrogen Ions. (Williams and Wilkins), 1923, Baltimore.
2. **Clark, W. M.,** and **Lubs, H. A.** J. Bact., 1917, ii, 1, 109, 191.
3. **Felton, L. D.** J. Biol. Chem., V. 46, p. 299, 1921.
4. **Bodine, J. H.,** and **Fink, D. E.** J. Gen. Phys., Vol. 7, p. 735, 1925.
5. **Michaelis, L.** Die Wasserstoffionenkonzentration, Berlin, 1914.

THE THERMOCOUPLE METHOD OF DETERMINING TEMPERATURES.*

WM. ROBINSON,
Division of Entomology, University of Minnesota.

USES AND ADVANTAGES.

The thermocouple is used in many different fields for the determination of temperatures. Physicists first employed this method in 1812, but at that time the process was a slow and tedious one. With improved apparatus the method became more practicable, and during recent years it has come into wide use both in the exact sciences and in the industries.

In biology the thermocouple method is also coming into more frequent use. It is very well adapted to entomology, and in fact there are occasions when temperatures cannot be taken practicably by any other means. With this method it is possible to determine temperatures of places which are otherwise inaccessible, as in an atmosphere of poisonous gas when fumigating, or in the soil, water or under the bark of trees. The internal temperature of insects under various conditions may also be found.

When the couple is placed in position, readings of any number of points may be taken quickly, and this may be continued over an extended period without disturbing the situation. The location, also, may be practically any distance away.

The thermocouple permits extreme accuracy, for with its accessory parts it forms an instrument of high precision and gives readings correct within one twenty-fifth of a degree if this is desired. An accuracy of one one-thousandth of a degree may be obtained but this requires especially sensitive equipment and is beyond the scope of the present article.

A very rapid response to temperature changes is characteristic of this method for the couple shows instantly any change large or small. This is necessary on such occasions as when recording heat of crystallization during freezing-point determinations. Another advantage is that temperatures are very

*Published with the approval of the Director as Paper No. 699, of the Journal Series of the Minnesota Agricultural Experiment Station.

distinctly indicated; and the galvanometer may be made so sensitive that a change of one degree in temperature will have a range of one inch or more on the scale.

The thermocouple system is simple and easy to operate and the accessory apparatus required is not unduly expensive. Probably if more were known about the subject it would lead to a greater use of this method in entomology. Following is a non-technical statement of the principles involved and the method of construction and operation.

The Principle of the Thermocouple.

If wires of any two dissimilar metals, copper and nickel for instance, are joined end to end, two connections called "thermo-electric junctions" will be formed as at A and B in Figure 1-a.

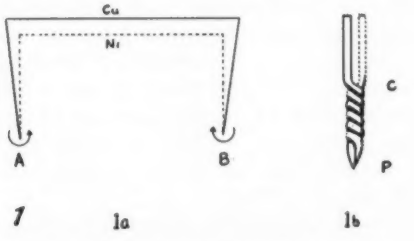


Fig. 1. 1-a, Two thermo-electric junctions.
1-b, Detail of junction.

These junctions are so named because when the two different metals are joined together a flow of electrons will take place from one metal to the other, in this case from copper to nickel. This flow of electrons results in a force called an "electromotive force" (e.m.f.) being set up at each junction; and the magnitude of this force *depends on the temperature.* If the temperatures of the two junctions are equal the e.m.f. will also be equal; and since the flow of electrons is from copper to nickel, as shown by the arrows in Figure 1-a, the two forces will be opposed to each other. Consequently there will be no current in the circuit. However, if the temperatures are different there will be a greater e.m.f. generated at the warm junction (with metals used in biology) resulting in a current around the circuit. The energy necessary to maintain the current is derived from the excess heat absorbed by the warm junction.

The current depends, therefore, upon a difference of temperature being maintained between the two junctions. The cold junction is kept in a known and constant temperature as in a mixture of ice and water in a thermos bottle, which can be held for hours at 0° C. The warm junction is then placed in contact with the material the temperature of which is to be determined. Since one temperature is known, and since the e.m.f. generated in the thermocouple depends directly upon a difference in temperature between the two junctions, the unknown temperature can readily be determined.

The Principle of the Potentiometer and the Pyrovolter.

In actual practice the unknown temperature can be ascertained very quickly by a few simple movements. However, it is usually well to know a little about the instruments used and the principles involved. The e.m.f. generated in the thermocouple can be measured in two ways: by the galvanometer and the potentiometer methods. The former measures the current direct and is the simpler method, but it involves certain errors due to the resistance of the lead wires, which resistance varies with the length and diameter of the leads. Errors also come in because of differences of temperature through which the leads pass.

Fortunately these errors are eliminated in an ingenious and satisfactory manner by the use of the potentiometer. With this instrument only the e.m.f. of the couple *and not the current* is measured. Consequently the leads (which are the copper wires connecting the junctions with the potentiometer) may be of any length and diameter and may pass through any variations of temperature without affecting the accuracy of the readings. In order to measure this e.m.f. it is balanced against a variable "difference of potential" (d.p.) in a circuit within the potentiometer, and the d.p. is known by means of a "standard cell."

A very compact and portable instrument results from a simplification of this method. It embodies what is called the pyrovolter principle where the use of the standard cell is avoided. By simply turning a knob until the galvanometer points to zero, the e.m.f. of the couple is first balanced against the d.p. of a fixed resistance within the instrument. Then with a second movement the connections are so changed that the galvano-

meter is inserted into the main circuit. A deflection is at once produced within the galvanometer and it indicates two things at the same time. It indicates first the d.p. which balanced the e.m.f. of the couple because the deflection is produced by the identical current that previously had produced the d.p. Secondly it indicates the temperature of the warm junction because the magnitude of the e.m.f. is dependent upon temperature difference, and the scale is marked to show degrees of temperature.

Simplicity of the Thermocouple Method.

Although it may appear at first glance to be rather complicated, this method is in reality quite simple and rapid, due

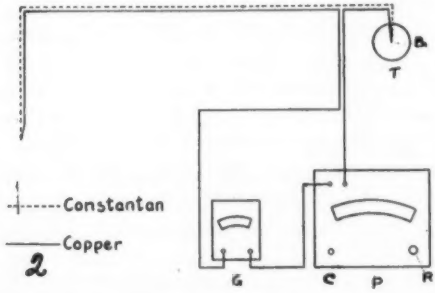


Fig. 2. Method of connecting couple for a single assembly.

largely to the excellent equipment now available. Complete outfits for this work may be obtained from various makers of scientific electrical equipment. The instrument embodying the pyrovolter modification is so constructed that it contains all the necessary parts for the work, except the outside galvanometer; and it is very satisfactory for use in biological work. When making the determination the two leads from the thermocouple are connected to the pyrovolter, through the outside galvanometer; the balancing e.m.f. is obtained by turning knob R, Figure 2, until the galvanometer points to zero; then a button is pressed and the deflection instantly indicates the desired temperature.

Construction of the Thermocouple.

The type of thermocouples required in biological work can be made very easily; and although couples for a great variety of purposes may be purchased complete from the various scientific electrical instrument companies, it is well to know how to make them in the laboratory. For the range of temperatures with which biologists are concerned the two metals used are copper and constantan. The latter is an alloy of 60% Cu and 40% Ni. Wire of these metals may be purchased in a number of gages and with silk, cotton or enamel insulation. Number twenty-eight gage has been found by the writer to be preferable for most purposes, and enamel insulation to be the most satisfactory.

A length of constantan wire, equal to the distance between the thermos bottle and the point where the temperature is to be determined, is taken together with a length of copper wire one foot longer. The insulation is removed from the ends for about one-half an inch; then one end of each wire is wound around the other as shown in Figure 1-b. The junction is next evenly soldered from the tip to the point of separation. A good method is to melt a little self-fluxing solder, as used in radio work, upon a clean side of a soldering iron and then to immerse the junction in the lead from C to P, Figure 1-b. This is to be the warm junction. The other end of the constantan wire is soldered in a similar manner to a piece of copper wire about twelve inches long; and this provides the cold junction. A thermocouple is then completed for a single assembly, Figure 2. If the object is to pierce the body of an insect to determine its internal temperature, the tip of the warm junction should be pointed by rubbing it lightly with a fine file, emery cloth or sandpaper, preferably under a pair of binocculars.

A small amount of surgeon's adhesive tape wound between and around the wires of the warm junction will give rigidity to the wires and serve as a handle if such is desired. The silk or cotton insulation of these fine wires soon wears off; therefore if that kind is used, coating it with a substance like shellac or quick drying varnish or enclosing the wires in a rubber tube is recommended to prevent short circuits. Enamelled wire does not require this treatment.

Two holes should be bored in the cork of the thermos bottle, one to hold a thermometer and the other to admit the thermocouple junction. This junction may be lowered directly into the ice and water, but it is much more preferable to enclose it in a piece of glass tubing, one end of which has been previously fused solid in a flame. After the point has been pushed down into the tube to the bottom the space in the tube should be filled with cotton to prevent air currents which would otherwise affect the temperature at that junction.

Single and Multiple Thermocouples.

For determinations of only one unknown temperature, the arrangement shown in Figure 2 will be satisfactory. The

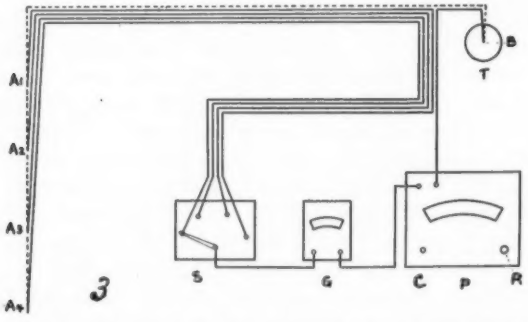


Fig. 3. Arrangement for multiple assembly with warm junctions in linear order.

junction A is the one to be inserted in the material. B is the cold junction in the thermos bottle T. The copper leads from the two junctions are connected to the potentiometer P and the outside galvanometer G. This latter instrument is strongly recommended in biological work for accuracy in determining when balanced conditions have been obtained. That is, when sufficient d.p. from the potentiometer has been opposed to the e.m.f. of the couple the outside galvanometer will point to zero; and not until that time should the temperature be taken. The distance from A to B may be any length required. The constantan wire in all the diagrams is represented by the broken line and the copper by the full line.

Frequently it is necessary to determine temperatures of two or more places without removing the junctions. It is quite feasible to do this and to take the readings over an extended period with only a slight modification of the couple. Two types of multiple couples may be constructed very easily. The one shown in Figure 3 is designed for use when the junctions are to be placed one after the other in a continuous arrangement.

Frequently it is necessary to push the couples into a mass of material and this can be done by using a metal pipe. The wires, unless enamelled, should be throughly insulated with shellac or varnish and the system tested before being drawn into the pipe. The junctions should always be insulated with electrician's tape or other material to prevent short circuits

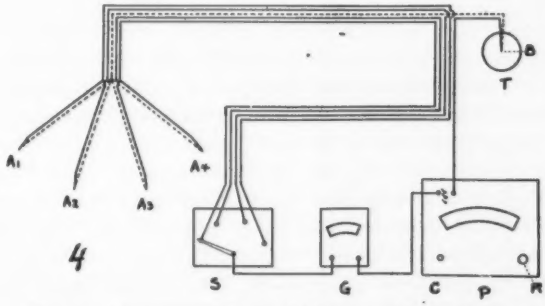


Fig. 4. Arrangement for multiple assembly with warm junctions scattered.

with the metal pipe. Air circulation within the pipe should be cut off, as previously mentioned, and this can be done easily by drawing into the pipe along with the thermocouple a cord with plugs of cotton placed in position two or three inches from each junction.

This particular arrangement records the temperature of the air around the junctions, and the air is affected by the temperature of the pipe in contact with the material to be tested. It is therefore merely a matter of each junction coming into equilibrium with that material. It is a comparatively slow process but is quite suitable for some purposes where the temperatures are to be taken over an extended period.

If the locations are accessible this type of couple may be installed by hand and not enclosed in a tube or pipe. It will then give instantaneous readings of temperature.

The other kind of multiple couple, as shown in Figure 4, is made with separated junctions, for use especially where the locations are scattered in various directions. The branches of constantan wire may be soldered to the main constantan wire at any desired or convenient place. The rotary switch S, Figures 3 and 4, is recommended. The plugs on the switch are numbered, and when the lead or copper wire from each junction is connected to its assigned plug, then individual readings can be taken very quickly; for only one junction can be in circuit at any one time, the others are brought in at will by moving the switch over the plugs.

Precautions.

Since this apparatus is exceedingly sensitive to temperature and will record very minute changes, it requires corresponding care when using it. Certain precautions are necessary, therefore, in order to get accurate and reliable results.

When about to use the apparatus, the accuracy of the assembly should be checked up by taking the temperature of, say, a bottle of water of known temperature. This has been found better than reading the temperature of the air. It is well to have a bottle of water for this purpose permanently in the laboratory, fitted with a cork and thermometer.

The outside galvanometer should always point to zero when not in circuit. Therefore before using it should always be checked up and if necessary adjusted to read zero.

If the junction has been used for piercing moist tissue, it should be cleaned after each determination by dipping it first in alcohol to remove water soluble material and then in ether to remove fats and alcohol. This is especially necessary when taking freezing-point determinations.

The temperature of the water in the thermos bottle should be carefully watched. The cork should have two holes, one to admit the junction and the other a thermometer. The bulb of the thermometer and the end of the junction should rest in the water at the same depth.

It should be remembered that the e.m.f. of the junction is set up *at the point of contact*, and that this point is where the

metals come together, namely at C, Figure 1-b, and not at the tip P. The length CP is merely to give strength to the junction and for convenience in piercing. Therefore in taking readings it is essential to have the point of contact C well within the material.

As soon as the reading has been taken the knob R should be turned back to cut off the current from the battery. If the knob is left turned on indefinitely the battery will be unduly weakened.

Procedure in Making a Temperature Determination.

The cold junction is placed in the thermos bottle filled with ice and water. The outside galvanometer is adjusted, if necessary, to read zero when at rest. The thermocouple is connected as shown in the diagram. The warm junction is placed in the bottle of water to check up on accuracy of set-up. The junction is quickly dried by dipping it in alcohol.

Up to this point the procedure has been preliminary to the temperature determination and, of course, it is necessary only when commencing operations. From this stage any number of determinations may be made quickly and simply as follows: Place the warm junction in the material to be tested and it will be observed that the outside galvanometer is immediately deflected from zero. Then turn the knob R forward until the galvanometer again points to zero, press down the button C and read the temperature indicated on the pyrovolter scale. Turn back the knob R.

Summary.

Some of the uses and advantages of the thermocouple method of determining temperatures are discussed, together with an outline of the principles involved. Detailed instructions are given for making thermocouples in the laboratory. The method of procedure in taking a reading is described and certain precautions are suggested in the use of the apparatus.

THE DEVELOPMENT OF THE PROVENTRICULUS OF PITYOGENES HOPKINSI SWAINE.

By James A. Beal, M. S.

Introduction.

The object of this paper is to describe the changes which take place in the proventriculus, of the bark beetle *Pityogenes hopkinsi* Sw. during the period of growth and development from early larval through pupal and adult stages respectively.

The proventriculus is a portion of the alimentary canal lying just anterior to the ventriculus or true stomach which in the adult bears on its internal surface a complicated apparatus consisting of teeth, grinding plates, and straining brushes. This is a chitinous structure, a secretion of the alimentary canal, located in the prothorax. Its function is probably the breaking up, grinding and straining of food which has been taken in by the insect.

A knowledge of this organ has considerable value in taxonomy. The characters of the proventriculus have been discussed in papers by Lindeman, Verhoeff, Sedlaczek, Nusslin, Fuchs, Hopkins, Swaine, and others; and these characters have been employed in arranging keys for determination of genera and even of species. Swaine* says, "I have found internal characters, especially of the proventriculus, of the greatest interest and of much practical value; but a wider study is apparently necessary, employing many genera and species, particularly many specimens in each species, before definite conclusions can be drawn."

The proventriculus is very complicated in structure and its development presents an extremely interesting problem from the standpoint of pure science. Doctor Otto Nusslin† is the only author who has ever described, even in a general way, the development of the proventriculus of any species of bark-beetle. The work which he did on this subject can be found in a German

*Swaine, J. M. 1918. Canadian Barkbeetles, Part II, page 34. Bull. 14, Dominion Depart. Agri.

†Nusslin, O. "Phylogenie und System der Borkenkafer." Zeitschrift fur wissenschaftliche Insectenbiologie, Vol. 7, 1911.

scientific publication. He describes in a very general way the development of this organ, using, to illustrate his descriptions, six original photomicrographs of four stages in *Ips typographus* and two of *Ips acuminatus*. Doctor E. P. Felt* shows, in Memoir VIII, N. Y. State Museum, two photomicrographs of *Pityogenes* sp. in the adult stage.

This problem, then, is one to which very little attention has been paid but which offers much of interest in the way of further study. The reason for selecting this particular species, *Pityogenes hopkinsi*, was because its life history and the methods of rearing this beetle under artificial conditions have been accurately worked out by Doctor M. W. Blackman.† It responds quickly to artificial heat and when brought into a warm room from winter temperature will become active in the course of a few minutes and will, if given an opportunity, begin operations for continuing its normal summer activities.

Procedure of Breeding and Rearing.

In order to work out such a problem it was necessary to secure large numbers of the specimens in each of the stages in which growth and development occur. To accomplish this the adult beetles were collected, as needed, from dead pine limbs in the field, placed on freshly cut green pine in breeding jars and kept at a constant temperature of approximately eighty degrees Fahrenheit. This was accomplished by the use of a large pasteboard box in which was placed an electric bulb, of sufficient voltage, to keep the temperature within at about eighty degrees Fahrenheit, thus serving as an incubator in which the breeding jars were kept at all times. Moist sand was placed in the jars and the bottom ends of the pine sticks were imbedded in the sand and the upper ends were coated with parafin. This method of handling the breeding material conserved the moisture long enough, under the high temperature, to allow the broods to develop successfully.

It was possible to obtain some larvæ, pupæ and adults in the field when the work was begun in September but as winter advanced it became more and more difficult to find them in

*Felt, E. P. 1906. "Insects Affecting Park and Woodland Trees," Plate 68, Fig. 4; P'ate 69, Fig. 1.

†Blackman, M. W. 1915. "Observations on the Life History and Habits of Pityogenes hopkinsi Swaine." Tech. Pub. No. 2, N. Y. State College of Forestry.

all stages, and finally the pupæ became so scarce that it was impossible to get enough with which to carry on the work. Although specimens winter over as adults and a few as larvæ, it would seem that almost none actually pass the winter as pupæ.

Adult beetles were collected every week and placed in new breeding jars so that a continuous supply of specimens in all stages were available simply by stripping the bark from the infested pine limbs and collecting the desired specimens.

As this species usually breeds only in the smooth bark of pine it was necessary to select pine limbs from one-half to two inches in diameter. It was possible to get larger sized limbs having smooth bark but they were not so easily handled in the breeding jars.

There are five larval instars; by that is meant five definite castings of the skin preceded by five short periods of growth. It was possible to place the larval specimens in their respective instars by the use of a table constructed by Doctor M. W. Blackman* in which it was shown that the width of the head is fairly definite for each instar. In part it is:

Instar	*Width of Head, mm.*
1	.300–.315
2	.345–.370
3	.412–.450
4	.475–.500
5	.520–.550

It then became a simple matter of measuring the width of the head of each of the larvæ, and placing them in their respective instars. A micrometer eye piece and compound microscope were used in making these measurements.

In order to secure pupæ of known ages large full grown larvæ were put into separate Stender dishes and examined daily for newly transformed pupæ. The selected specimens were larvæ from the fifth instar whose thoracic regions were swollen and enlarged and whose color was white due to cessation of feeding, thus presaging an immediate change to the pupal stage. Whenever new pupæ were found, they were also placed in other Stender dishes and examined daily until they reached the desired age. By this method it was found that the pupæ of this species, if kept under ideal conditions of moisture and

*Blackman, M. W. 1915. Technical publication No. 2 of the New York State College of Forestry, page 39.

at a temperature of about eighty degrees Fahrenheit, will transform to adults on the sixth day. Specimens of pupæ ranging in age from one to six days were secured in this manner and some were permitted to become callow adults to furnish specimens for study of the fully developed proventriculus as found in the adult beetle.

Technique of Preparing Microscopic Sections.

The method of handling specimens so delicate furnished considerable of a problem in itself and only after much experimentation with fixatives, stains, and imbedding materials was a satisfactory method worked out. The following is the method of killing, fixing and hardening, clearing, embedding, and staining, which gave the most satisfactory results with the specimens used. For suggestions regarding the histo-logic technique Lee's Vade-Mecum proved the most valuable reference.

Specimens were taken directly from their burrows and placed in Gilson's mixture which consists of:

Nitric acid, 46 per cent. strength	15 c. c.
Glacial acetic acid	4 c. c.
Corrosive sublimate	20 grms.
60 per cent. alcohol	100 c. c.
Distilled water	880 c. c.

This afforded a reliable and delicate fixation and left the tissue in a better condition than any of the other fixatives tried. Specimens remained in this fixative for twenty-four hours, after which they were removed and washed in water followed by a fifty percent alcohol solution and then run in the ordinary manner through the higher alcohols to ninety-five percent alcohol containing a few drops of iodine to remove the corrosive sublimate. Next they were put into a mixture of alcohol and ether fifty per cent each. From here they were placed into a two percent solution of celloidin, which was made by dissolving two grams of parloidin in a mixture of 49 c. c. of alcohol and the same of ether. After twenty-four hours the specimens were put for a similar period of time into a four per cent solution of celloidin and then removed and placed for five minutes in chloroform from which they were transferred to melted paraffin at 55 m.p. for five minutes and then imbedded in a small paraffin block by the drop method. The position of the specimens was indicated in the block of paraffin and the blocks were

trimmed, mounted, and cut in series by the use of a rotary microtome. The specimens were cut five micramillimeters and seven and one-half micramillimeters thick—thinner sections of this material being impossible to secure with the mixed paraffin-celloidin method because of the difference in firmness of the two imbedding materials used. The knife in cutting thinner sections tended to compress the paraffin and to buckle the celloidin which usually broke the specimens up to a considerable degree. The sections, when cut of the proper thickness, came off the knife ribbon fashion and were fastened to slides with Meyer's egg albumen. It was found best to float them on water and warm the slides gently to flatten them on the glass. Xylol was used to dissolve the paraffin. A number of stains were tried but all of the sections used were stained in haemalum made as follows:

Haematoxylin	1 grm.
Water	1 liter
Iodate of sodium	2 grms.
Alum	50 grms.

They were counterstained in Congo red, made by dissolving it in ninety per cent alcohol. They were then cleared in xylol and mounted in Canada balsam for further study.

As it was necessary to study whole preparations of the proventriculus of adult beetles in order to get the relative position of some of its parts, a number of the beetles were broken apart at the juncture of the thorax and abdomen and the exposed proventriculus teased from the prothorax, and then fixed in alcohol, cleared in creosote, and mounted on glass slides for observation. Some whole preparations were studied while they were floating in the creosote. This was very useful as it allowed them to be turned about in any desired position.

Specimens were cut both in cross-section and longitudinally and completed preparations were classed as to the larval instar represented, the age of the pupæ in days, or as adult beetles, including several whole preparations of the latter stage. The sectioned and mounted specimens were saved to be used in working out the development of the proventriculus, and drawings of the various stages were made to aid in clarifying the descriptions given herein.

Observations.

Larvæ of the first instar.

The proventriculus of the newly hatched larvæ shows, in cross section, indications of an outer layer of muscles, most of which appear, in relation to the proventriculus, to be circular muscles. Some, however, appear to be cut in cross-section, so are no doubt longitudinal muscles. This band of muscles is but a few cells in thickness and in some cases is not clearly distinguishable for the entire distance around the proventriculus. These muscles are more or less intermingled and cannot be differentiated into definite circular and longitudinal bands as are found in the higher animals and such as occur in the adult of this species.

Just within the muscular band is found a basement membrane which appears as a distinct line separating the muscular layer from the epitheial cells described in the following paragraph.

Next in order is a row or layer of simple columnar epithelial cells with their nuclei located near their basal ends, adjacent to the basement membrane. The nuclei stain blue with haemalum and are easily distinguished from the other parts of the cells. The basal ends of these cells contain the nucleus in which the chromatin network appears as dark blue thread-like structures. The cytoplasm, outside the nucleus, is finely granulated toward the proximal end, that is, next to the basement membrane, while towards its distal end it has more of a recticular structure. Covering the distal ends of the cells and lining the lumen is a relatively thin layer of chitinous substance which comes into direct contact with the food taken into the body. This chitinous layer entirely surrounds the lumen or central opening of the proventriculus.

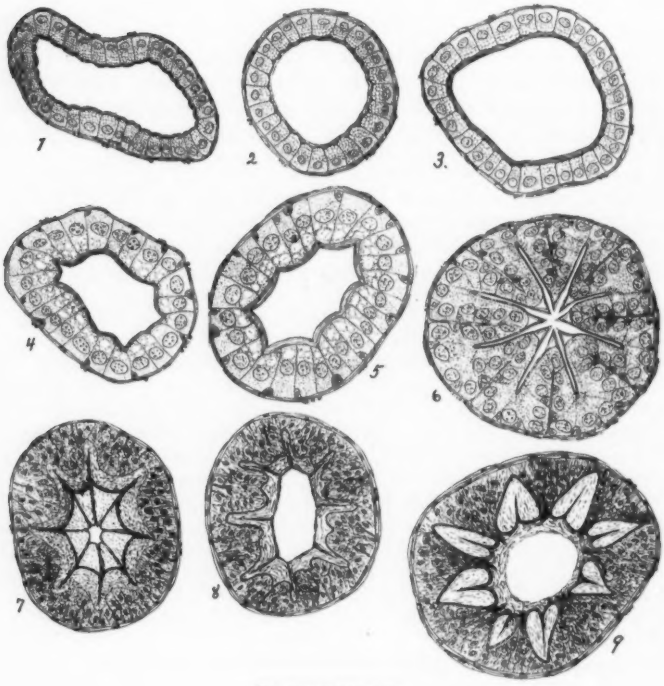
The parts then of the proventriculus of a very young larva are four in number, from the outside toward the lumen they are: the muscular layer, the basement membrane (not seen in cross-section except as a definite line separating muscle and epithelium), a layer of simple columnar epithelial cells, and an inner chitinous layer which is a secretion of the epithelial cells. These parts are shown in Figure 1.

Larvae of the second instar.

This stage shows conditions very similar to those found in the first stage larvæ except that the circular-longitudinal muscular layer is somewhat more prominent forming a more nearly complete band, and the chitinous membrane given off or formed at the internal extremities of the epithelial cells is somewhat wider than is found in any of the larvæ of the first stage. Figure 2.

Larvæ of the third instar.

This stage does not differ greatly from the two preceding stages except that the chitinous layer at the inner end of the epithelial cells is more in evidence and has become somewhat thicker than that found in the preceding stage. The simple columnar epithelial cells appear somewhat shortened in length and are more nearly cuboidal (square as



PROVENTRICULUS.

1. *Pityogenes hopkinsi* Sw., cross-section of larva of first instar ×266, showing outer incomplete muscular layer, basement membrane, a layer of simple columnar epithelial cells, and an inner chitinous layer.
2. *Pityogenes hopkinsi* Sw., cross-section of larva of second instar ×266, showing conditions similar to Figure 1.
3. *Pityogenes hopkinsi* Sw., cross-section of larva of third instar ×266, showing conditions similar to those found in Figures 1 and 2.
4. *Pityogenes hopkinsi* Sw., cross-section of larva of fourth instar ×266, showing addition of replacement cells at the base of the epithelial cells, and first indications of division in the epithelial layer.
5. *Pityogenes hopkinsi* Sw., cross-section of larva of fifth instar ×266, showing increase in number of replacement cells, and division of epithelial layer into eight distinct corrugations.
6. *Pityogenes hopkinsi* Sw., cross-section of newly transformed pupa ×266, showing increase in both number and bulk of epithelial cells, and infoldings in basement membrane.
7. *Pityogenes hopkinsi* Sw., cross-section of pupa one day old ×266, showing reduction in size of epithelial layer, and sloughing off of the semifluid chitinous secretion nearly filling the lumen.
8. *Pityogenes hopkinsi* Sw., cross-section of anterior region of proventriculus of pupa three days old ×266, showing divisions in epithelium at apices of corrugations.
9. *Pityogenes hopkinsi* Sw., cross-section of the posterior region of proventriculus of pupa three days old ×266, showing active secretion and pouring out of cell contents into lumen.

seen in cross-section) than those of the second stage. Up to this time there has been no noticeable increase in the number of cells making up the epithelial layer, but due probably to expansion the proventriculus appears somewhat enlarged and this naturally reduces the length at the same time increasing the width of the cells present. Illustrated in Figure 3.

LARVÆ OF THE FOURTH INSTAR.

In this stage there is a still further step in the thickening of the chitinous layer. The most apparent difference found here, however, is the addition of a few small cells in between the bases of the columnar epithelial cells. These new cells are very small and are probably formed to take the place of the earlier cells which may be worn out or lost in growth and development and to aid in the great increase in the number of epithelial cells which occurs later. These cells are called replacement cells.

In the distal ends of the epithelial cells the reticulum appears very much coarser than in any of the preceding stages and it is a little more transparent. These small globules thus indicated are probably secretions in the formative stage which are to be used in the later development of the proventriculus.

In this stage the epithelial and chitinous layers, as seen in cross-section, are not the regular circular bands found in the preceding stages but both layers are more or less folded or corrugated thus producing the appearance shown in Figure 4. There is an occasional deep fold which reaches part way through the layer of epithelial cells toward the circular muscular layer. These folds occur at irregular intervals of three to five cells. The deepest reach one-fourth of the way down the cells toward the basal ends. These deeper and therefore more apparent divisions probably indicate a group formation of cells for a definite purpose, the significance of which will be seen later.

LARVÆ OF THE FIFTH INSTAR.

A very radical change occurs during the late fourth and fifth instar. It is during these stages that the insect undergoes probably its greatest amount of development while it is still taking food. It is then that it eats great quantities of food in preparation for its pupal existence. It builds up a surplus of tissues which prepares it for the very fundamental changes which take place during the pupal period. As the taking of food into the body of the pupa is a physical impossibility, it must depend on that which has been stored up previously.

The replacement cells are more numerous in the fifth larval stage than they were in the fourth instar. They still occupy their characteristic position between the bases of the cells as seen in cross-section.

In the fifth instar the deeper corrugations which first appeared in the fourth stage are more regular in arrangement and the epithelial layer is now separated into eight definite folds and elevations making, in cross-section, eight groups of cells which contain on their outer surface the large globules of secretion which later go to make up the newly developing parts.

The chitinous layer appears to be approximately the same width as that of the preceding stage. The muscular band shows no perceptible change in this stage of the development. An illustration of the parts as described under the fifth larval instar may be found in Figure 5.

EARLY PUPAL STAGE.

It perhaps may be well to mention here that conditions as described for this stage are sometimes, though rarely, found in the late fifth larval instar. There is an occasional overlapping of one stage into the next, and this is equally true of all of the other stages, for, like variations in the age of maturity of man, we find a difference according to individuals. However, a great many specimens were studied and the illustrations were taken from specimens which showed the most typical conditions.

In the early pupal period there appears a markedly different arrangement of the muscular layer, epithelial cells, and chitinous band, but their general relations to each other are similar. The cells which become grouped into eight longitudinal ridges or corrugations in the last larval instar have been further separated from each other. The replacement cells have proliferated to such an extent as now to produce a true stratified columnar epithelium, only the distal cells being of the columnar variety while the others are crowded between this outer layer and the basement membrane forming a mass of cells in no definite layers.

As shown in Figure 6., there has been a folding-in of the original epithelial layer. The bases of the columnar cells have torn away from the basement membrane and in so doing have retained parts of the membrane which appears in cross-sections of this stage as a definite line extending in as an axis of each corrugation. This is evident in very few of the later stages and is probably obscured by the dense crowding of the cells which are at this stage producing a great amount of formative secretion which is used, in the later stages, for the development of parts of the proventriculus. At the distal ends of the corrugations there appears to be a flaking-off of the chitinous layer into a flocculent or semifluid substance nearly filling the remaining lumen. The epithelium at its more distal portions has shrunken slightly away from the chitinous layer.

The outer muscular layer having no additional function beyond that of the preceding stage is of the same size and condition as previously noted. The changes which have taken place from the preceding stage to the one just described are shown in Figure 6.

PUPÆ ONE AND TWO DAYS OLD.

A rapid change takes place in the growth of organs in insects from one day to the next. In this stage there is a sloughing off of the secretion from the distal ends of the columnar cells of the epithelial layer, which are the only exposed cells. This, as it comes off, appears as a very broad band of chitinous material in a semi-fluid condition. The outline of the lumen remains the same as in the newly transformed pupæ but

the groups of cells themselves occupy considerably less space than before. The cells are reduced in size by the discharge of their contained secretion, and the space thus gained is filled by this secretion.

The cells in the epithelial layer are more numerous—the additional ones having arisen from the cell division of the earlier replacement cells. In this stage the replacement cells cannot be distinguished from the original epithelial cells as they are diffused throughout the epithelium and are of approximately the same size as the reduced epithelial cells. The muscular layer shows no new development.

The preparation of the two day old pupæ are so similar to those of the one-day old pupæ that no illustrations seemed necessary or advisable and as development had apparently proceeded but very little, no description need be given. Figure 7 illustrates the condition as found in one and two day old pupæ.

PUPÆ THREE DAYS OLD.

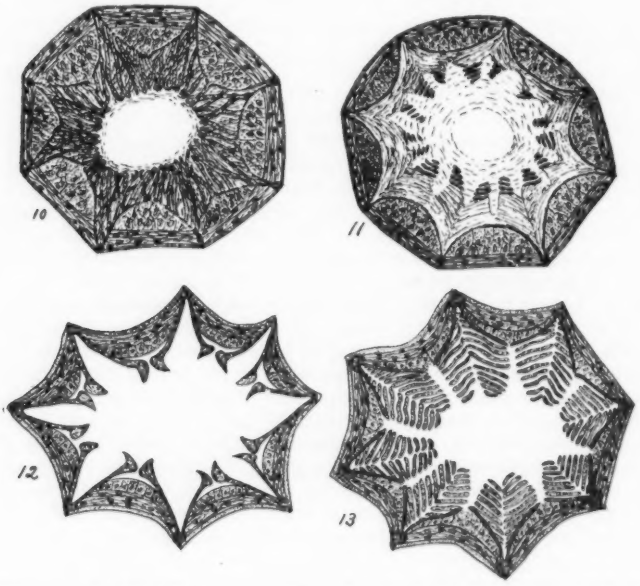
Up to this stage the development of the proventriculus has been uniform throughout its length but now there appears a difference in the anterior and posterior regions. The condition found in the forepart of the proventriculus, Figure 8, is relatively simple but the structure becomes more complicated in the posterior region as is shown in Figure 9.

A cross-section in the anterior region of the proventriculus of a three day old pupa is very similar to conditions found in the one and two day old pupæ except that there is an additional grooving of the distal end of each of the eight distinct groups of cells. This partial division takes place in the epithelium and longitudinally marks off the corrugation into two nearly equal parts, which seems to indicate here the beginning of the formation of something further. The wide band of membraneous chitin persists but the distal portion appears to have shrunken away, leaving a larger central opening or lumen. The condition of the epithelium is similar to that described for pupal stages one and two, being made up of many cells forming a stratified columnar epithelial layer. The circular muscular layer shows no additional changes.

A section taken from the posterior region of the proventriculus of a three day old pupæ shows a remarkable difference from a section of the anterior region of the same specimen. It also differs considerably from sections through the posterior regions of younger stages of pupæ. It is plain in this stage that there has been a decidedly active secretion from the cells at the apices of the corrugations. This is accomplished by the pouring out of a large amount of the formative secretion already described as occuring within the cells. It passes out in the form of a stringy semifluid substance. The cells having given up considerable of their contents, are much reduced in size and the material secreted by them occupies all of the resulting space except a central cavity or lumen about equal in size to that found in the anterior region of the proventriculus of the same age pupæ. Most of the reduced columnar epithelial cells are arranged in rows just proximal to the viscid or semifluid chitinous secretions, while the other epithelial cells which are also much reduced in size and are of irregular shapes make up the remaining epithelial layer with apparently no definite arrangement.

The outer muscular layer is of about the same thickness as found in the two day old pupæ, but has increased in size to conform to the increase in the size of the proventriculus.

In this stage the first extremely large, increase in the size of the proventriculus takes place and the area of a cross-section from a three day old pupa is more than twice that from either a one or a two-day old pupa—the diameter of such a cross-section being about one third greater than that of the preceding stage.



10. *Pityogenes hopkinsi* Sw., cross-section of posterior region of proventriculus of pupa four days old ×266, showing reduction in number and bulk of epithelial cells, strands of semifluid chitinous secretion, the much enlarged muscular layer, and the chitinous layer extending out into the muscular layer.
11. *Pityogenes hopkinsi* Sw., cross-section through posterior region of proventriculus of pupa five days old × 266, showing semifluid secretion near epithelial layer, and hardened portions of tips of forming plates more distal to it.
12. *Pityogenes hopkinsi* Sw., cross-section of anterior region of proventriculus of adult × 266, showing well-formed cutting teeth, reduced epithelium, a wide circular muscular layer, and an outer narrower layer of longitudinal muscles.
13. *Pityogenes hopkinsi* Sw., cross-section of posterior region of proventriculus of adult ×266, showing the edges of well-formed plates.

Outline drawings of Figures 1–13 inclusive and Figure 15, were made with a cameralucidia set at 70, using a ×6 ocular and a ×44 objective. Details were made under a ×95 oil of immersion lens with a ×10 ocular. The magnification was figured with a stage micrometer.

PUPÆ FOUR DAYS OLD.

This stage presents a still further complicated formation of new parts and shows a radical change from the three day old pupæ.

In the anterior portion of the proventriculus the change consists in the formation of teeth at the apices of the corrugations where the grooving occurred. The reason for the subdivision of each epithelial thickening is now apparent as from each of the subdivisions is now secreted a row of chitinous teeth. From each subdivision projections of the chitin appear which are plainly teeth in the process of formation. Their proximal portions are capable of taking some stain yet, but the distal edge and tips are more firm and show clearly the yellowish coloration characteristic of hardened chitin. As shown in cross-section, two large teeth in the formative stage are evident at the apex of each of the eight groups of cells.

In the posterior region the epithelial cells have been further reduced, as they also have in the anterior region, and a narrow band of more definite chitin is plainly seen in their distal surfaces and sides. The originally continuous layer of epithelium is now separated as each fold between the eight corrugations is lined by chitinous secretions which extend through the epithelium clear down into the muscular layer. This is due no doubt to the increase in size of the chitinous structure within the proventriculus which causes them to extend out beyond their former limits. The semi-fluid which was poured out from the epithelial cells in the preceding stage of the three day old pupæ is now arranged more definitely into strands interwoven and crossed. These structures appear to be arranging themselves into rake-like teeth and plate-like brushes.

The chitinous layer is open at the point where the excessive secreting activity occurred in the three day old pupæ, that is at the apices of the corrugations. At the tips of the forming strands there appears a quantity of the unformed still semifluid chitinous material as in the preceding stages. The epithelial layer is very much reduced by this time.

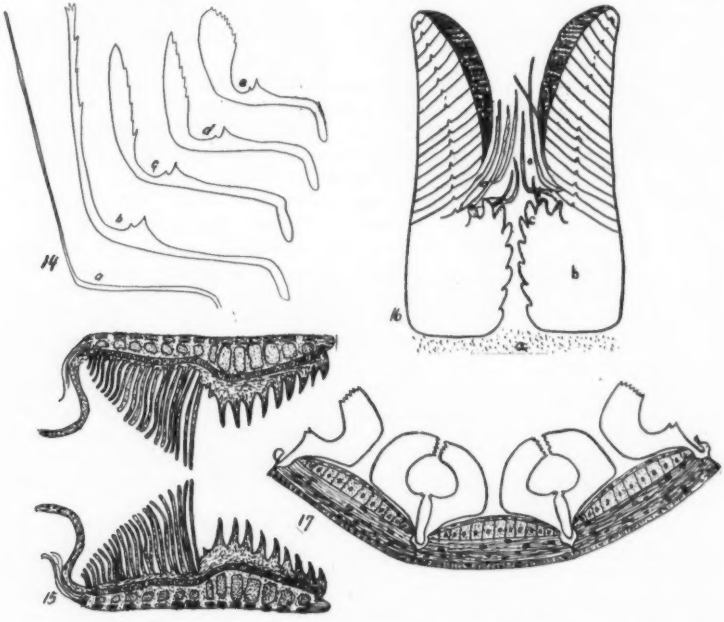
The circular muscular layer has become much thickened but longitudinal muscles are still very little in evidence. The increase in the size of the muscular layer is probably due to the necessity of additional muscles properly to operate the forming teeth, plates, and brushes. The significance of this will appear later. A cross-section through the forming plates, rakers, and brushes, is shown in Figure 10.

PUPÆ FIVE DAYS OLD.

In the five day old pupæ the formation of parts of the plate-like structures from the secreted semifluid chitin is very plainly seen as shown in Figure 11. They are arranged in slanting rows and in cross-section they appear as a number of loose plates located well out in the lumen. Apparently they have risen from a portion of the secreted substance poured out into the lumen by the epithelial cells. They thus originate directly opposite the eight primary corrugations. As only the well defined edges of the plates can be found at the distal

portions of the secreted substance, it may be properly assumed that the more distal parts of the plates are the first to harden into distinct chitinous structures. The more distal parts of the plates which are the first formed and are therefore firm and hard show very plainly, while the more newly formed portions which are still in the viscid state are not so apparent. These appear as a more or less flocculent material between the well defined edges and the epithelial tissue. There is also a general sloughing off of unformed chitinous material which appears as a flocculent formation and which only partially fills the lumen.

The chitinous layer next to the epithelial cells stains more densely than the less recently secreted portion distal to it and is probably in a



14. *Pityogenes hopkinsi* Sw., parts of proventriculus of adult greatly enlarged. (a) Straining bristle, (b) obstructing bristle, (c), (d), and (e), plate-like brushes.
15. *Pityogenes hopkinsi* Sw., longitudinal section of proventriculus of adult ×266. Anterior region is toward the right. Showing the arrangement of the various structures as seen in section. Note the wide band of circular muscles and the narrower band of longitudinal muscles.
16. *Pityogenes hopkinsi* Sw., diagramatic drawing of radial segment taken from proventriculus of adult greatly enlarged, showing relation of parts.
17. *Pityogenes hopkinsi* Sw., diagramatic drawing of portion of cross-section of proventriculus of adult greatly enlarged, showing method of attachment of plates into circular and longitudinal muscles.

semi-fluid condition. As in the preceding stage, the chitinous structure reaches, at the points of the folds, well into the muscular layer.

The circular muscular layer is considerably enlarged from earlier stages, but is similar to that found in pupæ four days of age.

ADULT STAGE.

On the sixth day the pupæ were found to transform to adults, sections of which showed clearly the final product of the elaborate process of development. This process includes the building up of many cells in preparation for the secretion of the complicated proventricular apparatus. Then followed the formation of these structures from the secretions of the epithelial cells. This was accomplished by a reduction in the epithelial elements as the cells were used up in the production of a relatively great amount of chitinous material in the course of a few days. Also coincident with these changes a great elaboration of the muscular layer takes place. This is a very essential part of the proventriculus as this organ is composed of sloping teeth, grinding plates, and straining brushes, and its equipment with strong muscles is very necessary for the performance of its functions.

A cross-section of the anterior region conforms in general outline to a similar section of the pupal stages already described. It consists of eight divisions of epithelial cells, separated by eight grooves extending to the muscular band, which at this stage is as large as the fifth pupal stage. In longitudinal section, there appears a narrow outer band of longitudinal muscles and an inner much wider, band of circular muscles. Figure 15. This formation of two definite layers is probably brought about by a proliferation and rearrangement in the original muscle cells. Within the inner muscular layer, the epithelial layer is represented by a few remaining epithelial cells. In some cases they are almost completely absent. Just within this layer is a very distinct chitinous plate having at the apex of each corrugation a pair of heavy sharp chitinous projections which point inward and backward. In cross-section Figure 12., they form a very formidable looking set of teeth.

The posterior portion of the proventriculus of the adult as seen in cross-section presents in outline form the same aspect as seen in the anterior region just described. The muscular layer is similar in size and structure, being divided into an outer longitudinal and an inner circular layer. As seen in cross-section this is not as evident as found in the anterior region, but when cut longitudinally the two muscular layers are very apparent. (Figure 15).

The chitinous layer separating the epithelial layer from the chewing plates is very evidently in the same relative position as found in the anterior region. Well formed plates such as those beginning to form in the fifth pupal stage are shown in cross-section of the adult beetle. These plates arise from an intermedian line between the apices of the corrugations.

The proventriculus of the adult *Pityogenes hopkinsi* is a very complicated structure. It is barrel-shaped when seen in whole preparations. It is radially symetrical being made up of eight sections which are som divided that each section is bilaterally symmetrical.

It seems advisable to begin at the anterior end of one of the halves of the eight bilaterally symmetrical sections and describe in detail the parts in the order in which they occur; that is, the parts which, when in their normal position, would be met in passing from anterior to posterior. It will be necessary to describe but one-half of this section as they are divided longitudinally so that they are bilaterally symmetrical.

From the anterior to the posterior are found: first the hair-like bristles on the crop. (The crop is a sac-like structure which is lined with chitin, as four days boiling in potassium hydroxide failed to dissolve it). On its inner side are found a great many tiny hair-like bristles whose function is uncertain. Next in order is the first part of the true proventriculus. Figure 16 b. It is a large chewing plate the median edge of which is lined with a row of cutting teeth. These teeth are quite heavy and coarse near the front and become larger and coarser toward the rear of the plate. They all slope backward. Posteriorly these teeth are found also extending circumferentially part way toward the intermedian line as shown in Figure 16 c. The side of the chewing plate divides near the intermedian line forming chitinous projections which pass out through the surrounding plate of chitin and fasten in the circular and longitudinal band of muscles.

At the rear of the large chewing plates arises a set of fine bristles. These are of varying length and are almost hair-like. They are simple in structure and possess no additional spines or barbs. Figure 14 a.

Next in order is found a set of obstructing bristles. These bristles are long, usually forked at the distal ends, and bear spurs and barbs along their sides (the side toward the lumen). Near the base of each rake-like bristle the shaft is widened to form a large flat plate-like spine armed with two barbs. This, when placed side by side with its neighboring plate, forms a row of sloping teeth which is inclined toward the rear of the proventriculus. The basal end of the obstructing bristle passes through the chitinous plate which lies next to the epithelium of the proventriculus, and attaches in the circular and longitudinal muscular layer forming the outer layer. These are illustrated in Figure 14 b.

Posterior to the obstructing bristles just described there is a series of broader plate-like or leaf-like structures the edges of which are fringed with spines giving them a bristle-like appearance. These structures bear near their basal ends the same type of flattened sloping teeth as described for the obstructing bristles. The mode of attachment is also the same as is found in the preceding case. Distal to the basal section, however, the two structures are very different. The more posterior structure distally forms a plate instead of a bristle and the distal edge of this plate bears more spines than does the rake-like obstructing bristle. At the point where the plates and the bristles meet the former are but one-half the length of the latter. These brush-like plates, however, generally become shorter and still more brush-like as they are followed toward the posterior. These are illustrated in Figure 14 c, d, e, but there are types which intergrade between these. The plates are attached to the muscular layers in the same manner as the plates and bristles which have already been described. They also

bear the sloping teeth near their ends. These sloping teeth which occur on all the brushes, bristles, and plates, at the same relative position, form a complete row. When the plates are in position, this row extends longitudinally the length of the proventriculus, posterior to the large chewing plates.

GENERAL POSITION AND RELATION TO BODY.

It is interesting to note the structure and position of each of the parts described as some indication to their purpose may be found by such a study.

The crop is a bag-like structure anterior to the proventriculus which serves to hold food particles taken into the body. While the food is in the crop, it undergoes a certain amount of maceration and preliminary digestion before it is passed on to the proventriculus. The presence of a crop allows the insect to store a considerable quantity of food which later passes on through the cutting and grinding proventriculus as this is able to take care of it.

The chewing plates with the cutting teeth on their median margins are attached to the muscular layers by chitinous projections which pass through the surrounding chitinous layer to the muscles. Contraction of the circular muscles drives the entire plate inward toward the lumen. A similar action of all of the plates at the same time considerably reduces the size of the lumen and brings the teeth in contact with the contents of the proventriculus. This results in the further comminution of the woody particles already chewed up by the mandibles and macerated in the crop. Thus contraction of the circular muscles drives the teeth inward. When the muscles relax the elasticity of the chitinous plate causes them to assume their former position. The mere fact that the teeth slope backward tends to drive the food in the same direction. The contraction and relaxation of the outer band of longitudinal muscles from front to rear in coordination with the circular muscles, causes a peristalic wave to pass backward in the proventriculus and consequently causes the food to pass in the same direction. The teeth on the edge of each chewing plate meet a similar set of cutting teeth on the edge of the plate making up the other half of the section. Thus these teeth work in opposition to each other and the result is an effective chewing up of the contained woody material. Following the chewing plates which have cutting teeth are the hair-like bristles the function of which is probably the straining of food particles. They serve to keep the larger particles back where the teeth can cut them small enough to be of use to the rest of the organism and at the same time to allow the already finely divided particles to pass on posteriorly.

Next are the rake-like obstructing bristles which probably serve about the same purpose as the hair-like bristles, keeping the larger food particles from passing through without further cutting. These bristles may act as a sort of supporting rack for the hair-like strainers anterior to them and serve to hold them in position against any pressure which may be exerted by the food. The rake-like obstructing bristles are also attached outside in the muscular layer and are capable of con-

siderable movement. Their teeth may serve to aid in further breaking up the food, acting on the smaller particles just as the cutting teeth acted upon the coarser ones.

Posterior to the obstructing brushes are the plate-like structures the edges of which are fringed with fine spines making them appear brush-like. The basal ends of these plates are fastened in exactly the same manner as the bristles just described in the preceding paragraph. The contraction of the muscles drives the sharp toothed edge of the plates inward and together, much as in the case of the large cutting teeth. The more anterior of these plates have teeth on them capable of considerable cutting while in the posterior region they are more brush-like. It is probable that some grinding of food material takes place in the more posterior region of the proventriculus where the plate-like brushes occur. The basal ends of these plates pass outward and fasten to the circular and the longitudinal layer of muscles so that without doubt there is movement at least in two planes.

Conclusion.

It has been demonstrated in this paper that during the first three larval instars there is little change in the proventriculus of *Pityogenes hopkinsi*. It consists of a layer of simple columnar epithelium the distal ends of which are covered by a thin layer of chitin. Occurring at the base of this epithelial layer is a basement membrane which separates the epithelium from an outer muscular layer. This layer is made up of intermingled circular and longitudinal muscles, the former being more in evidence.

It is in the fourth larval stage that the first actual indications of any new developments are found. In this stage the addition of a few replacement cells occurs and changes in the arrangement of the epithelium begin which later divide it into eight corrugations. This process is continued through the fifth larval stage and during the first pupal stage. The replacement cells divide and redivide, producing many cells which are arranged to form a typical stratified columnar epithelium, in place of the simple layer of the early larvæ. This stratified epithelium is not uniform in thickness but is arranged to form eight distinct thickenings or corrugations extending lengthwise of the proventriculus.

In the first few days of the pupal stage the epithelium of the proventriculus becomes very active, filling a considerable part of the lumen with its secretion which is later to be used in the formation of new parts. As this arises during the first three days of pupal life it appears as a flocculent mass—apparently

of a viscous consistency—and fills a considerable portion of the lumen.

From this formless mass the complicated chitinous structures of the proventriculus are formed during the last few days of pupal life. As it hardens the secretion takes the form of teeth, bristles, and variously modified plates.

A study of the later pupal stages shows that these chitinous structures begin to harden and take form at the tip first, i. e. at the portion farthest from the epithelium and nearest the lumen. This is demonstrated by a difference in staining power—the soft newly secreted chitin taking the Congo-red stain readily while the hardened chitin is impervious to stains.

With the beginning of secretory activity there is a great change in the epithelium. The distal ends of the larger columnar cells are apparently ruptured and the semi-fluid chitin streams from them. The cells are not only reduced in size by this but many are entirely used up as there is not only a reduction in the bulk of the epithelium by the time the pupal stage is completed, but an actual reduction in the number of cells.

In about the fourth day of pupal life a decided increase in the muscular layer is noticeable. Previously this has been inconspicuous and apparently little changed from the conditions in larvæ of the first instar. But in the late pupæ this layer is not only immensly thickened but is reorganized so as to form a definite inner circular and an outer longitudinal layer.

The circular layer is not a continous band but is divided into eight segments corresponding to the eight corrugations of the epithelium and the eight radial parts of the chitinous apparatus. These segments attach to the bases of the chitinous structures which extend out through the epithelium at an interradius (i. e. at each depression separating the corrugations).

The six day old pupæ change to adults and the proventriculus becomes fully developed. The epithelium is so nearly reduced that it is difficult to locate it at some places. All parts of the proventriculus—chewing plates, cutting teeth, straining bristles, obstructing bristles, sloping teeth, and plate-like brushes—are fully formed. They all slope toward the rear, but the straining bristles and the obstructing bristles are more nearly perpendicular to the basal chitinous band than are any of the other parts.

SOME OBSERVATIONS ON THE LEAF-MINING FLEA-BEETLE DIBOLIA BOREALIS CHEVROLAT.

By Helen Reed.

The plantain flea-beetle was first described by Chevrolat in 1844 as *Dibolia borealis*. It was later described by Melsheimer in 1847 as *Dibolia aera*, which synonym occurs very frequently in early American entomological journals.

It has at various times attracted attention by its rather conspicuous depredations on our common plantain. Scudder (1878) quotes from a letter from Professor F. H. Storer of Jamaica Plain, Mass . . . . . "In the latter part of May, 1876, it was next to impossible to discover a single leaf of plantain that was not completely riddled by beetles (Dibolia aera Melsh) ". Several thousands from all sorts of situations had passed through his hands and the only perfect ones he could find were from particularly cold, sunless places on the north side of buildings.

Horn (1889) says "This beetle is so well known as not to require special comment." Patch (1908) gives some notes on the life history and says of its occurrence "Every season the bronze green flea-beetle of the plantain is found feeding upon the leaves of this plant early in the season and again later in the summer." Nevertheless careful observations on the habits and life cycle have never apparently been recorded.

The species is very abundant on the Cornell University Campus at Ithaca, and it was there that the present study was made.*

Host Plants: Both larvæ and adults, appear to feed exclusively on broad leaved plantain (*Plantago major*). Feeding sears, frass, and mines have never been observed on the narrow leaved plantain, or any other common weed on the Campus at Cornell, where the preferred food is so abundant. However in the laboratory with no other food supply at hand, larvæ have mined the leaves of the narrow leaved species. This species has not adapted itself to the miner. It quickly blackens in the mined area, and later shrivels and dies.

*The author wishes to express her appreciation to Dr. James G. Needham, under whose direction the work was carried on.

Leaves of the broad leaved species, if not inhabited by too many miners, do not suffer; the plant has accommodated itself beautifully to ordinary infestation. However if there are too many tenants, the leaf is often killed and in some cases even the entire plant. The latter condition is unnatural, for the adults ordinarily do not deposit enough eggs on any one plant to kill it.

A curious response of the plantain leaf to the presence of the eggs of the beetle was observed. About the fifth day after the eggs were deposited, a sort of "humping up" of the eggs was noticed. This elevation became more noticeable on the succeeding days. It was found that the plant was forming a tissue under the egg similar to that of a gall. The larvæ were unhampered by it, and after burrowing down through the excess tissue, formed their usual mine.

Methods of Rearing: To observe copulation and oviposition, mating pairs were captured in the field and confined to breeding jars for observation.

The mining activities of the larvæ, as well as data on the number of molts, were determined by transferring newly hatched larvæ to fresh uninfested leaves. These leaves were kept in water in a moist chamber. This proved perfectly satisfactory.

The larvæ, when ready to enter the ground, were placed in a small quantity of fine earth in a watch glass. During the prepupal and pupal periods the soil was kept moist and the watch glasses themselves were kept in moist chambers. Using this method, it was very easy to examine the inhabitant daily.

Summary of the Life History.

Presumably these beetles spend the winter as adults—as do most of the Chrysomelidæ—particularly the tribe of flea beetles, although definite observations have not been made. Since they pupate very near the surface of the ground, and since the period of pupation is so short, it is very unlikely that the species could hibernate as pupæ.

Adults began to appear on the Campus at Ithaca about the third week in May. Pairs were captured in copulation as early as May 18th. Evidently copulation had previously occurred in some cases for newly laid eggs were found on May 17th. No unhatched eggs were found in the field after July 1st,

and during the week previous the only ones found were in cold, sunless places. The oviposition period for the brood extends over a period of about six weeks, though individual hibernating adults do not live for so long a period.

The season of 1926 was unusually late in this vicinity; according to Weather Bureau reports two weeks later than ordinary years.

The duration of the egg stage varies from 8 to 10 days under most favorable conditions. The larval period varies greatly with weather conditions; under most favorable ones it extends over a period of about 14 days, during which time the larvæ molt twice. When full grown, they make a slit in the epidermis of the leaf, and make their way into the ground. Here they form an oval pupal cell, in which they spend from 5 to 9 days as prepupæ, and from 9 to 12 days as pupæ. The adults emerge from the ground fully colored and chitinized and begin to feed immediately. There appears to be but one generation a year since no mating occurs in the new brood.

In a breeding jar, in which conditions were kept as nearly like those of the open as possible, the complete life cycle took place in 45 days. The egg stage appears normally to cover a period of 10 days, larva 15 days, prepupa 8 days and pupa 12 days.

Hibernating adults, even in the coldest, most sunless situations, were all dead by the middle of July, at which time adults of the new generation had already appeared on the warmer southern exposure.

Length of Different Stages.

Under most favorable conditions out of doors as well as in the laboratory, eggs were hatched in 8 to 10 days. Temperature and moisture apparently have considerable effect upon the length of this stage. Both dryness and cold prolong the period. Certain eggs laid during very dry weather did not hatch.

The first molt takes place on the fourth or fifth day. The second molt takes place on the seventh or eighth day; the duration of this period is therefore about three days. The length of the third larval instar varies greatly under different conditions. The first larvæ hatched in the laboratory left the leaf to enter the ground at the end of fourteen days, during all of which time they fed actively. Later in the season certain

larvæ, after two weeks of active feeding remained a week or ten days in a quiescent stage in the leaf. Records were kept of these particular larvæ and it was found that they required as long a prepupal period as larvæ, leaving the leaf at the end of the two weeks. Weather conditions again affect the length of the period.

The length of the prepupal period varies from 5 to 9 days, while 9 to 12 days are spent as a pupa.

Description of Different Stages.

Egg: (Plate XXVII, Fig. 9)—Light golden brown; ovate and flattened somewhat on uppermost surface. Length about .67 mm.; greatest width .32 mm. Surface covered with minute indentations.

The eggs are commonly deposited upon the upper surface of the plantain leaf (*Plantago major*), although the writer in a few instances has observed eggs on the under surface of the leaf.

The female eats out a small area on the leaf leaving the lower epidermis and some of the spongy cells. She then circles about the opening until she is in a proper position to insert the egg into the depression, slightly larger than the egg itself; a single egg is inserted together with some excretory material. At first the entire mass is a pale amber color; in less than fifteen minutes the excrement hardens and darkens and forms a roof-like covering to which the egg adheres. The beetles were not at all hesitant about oviposition in the laboratory. When the larva is ready to emerge it leaves the shell and directly begins its characteristic habit of mining, without appearing on the surface of the leaf.

Larva: (Plate XXVII, Figs. 1 and 2)—The length of the mature larva varies from 5.75 to 6 mm.; the head capsule measures .5 mm. in width. The general body color is a deep yellow. The body and head are flattened dorso-ventrally; the thoracic and abdominal segments have distinct lateral processes or tubercules.

The head (Plate XXVII, Figs. 4 to 8) is deeply notched behing, wedge-shaped in front and projects back into the prothorax for about a third of its length. The mandibles are large, thin and flattened. The prominent maxillary palpi are three segmented. The antennæ are relatively small and three segmented. Ocelli are wanting. The head is very dark brown, nearly black; the dorsal and ventral prothoracic plates are somewhat lighter in color.

On both the meso and metathoracic segments are found a pair of lateral grayish kidney-shaped spots bearing setæ. The legs are well developed and composed of five segments. The distal segment bears a single claw and a pulvillus.

The abdomen is composed of ten segments, the 9th and 10th are much reduced. (Plate XXVII, Fig. 3). The 10th segment is readily seen only in a lateral view. A single median anal prop-leg is borne by the 10th abdominal segment. Abdominal setæ in more or less

regular transverse rows are present on each segment, a double row dorsally, a single row ventrally. The whole body is covered with small grayish oval spots.

When the larva first hatches from the egg it is yellow. The color gradually changes to a creamy white, which color is retained until the last part of the third larval instar, when it gradually becomes a deep yellow. The head in the first and second instars is proportionately much larger in comparison with the size of the body. The head capsule of the first instar measures .25 mm., the second instar .38 mm.

In 1879 Comstock described the larva of *Dibolia aerea* (—*D. borealis*). It is possible he has described a different insect, since the larva studied in this investigation differed markedly from his characterization. The outstanding differences are shown by the following table:

	Comstock's Description.	*Larva Studied.*
1.	Length, 8 mm	Less than 6 mm.
2.	Color white (full grown)	Yellow.
3.	Second and third thoracic segments with transverse grayish spots	With lateral longitudinal grayish spots.
4.	Thoracic subdorsal spot	No subdorsal spot.
5.	Small round darker spots on second and third thoracic segments	None.
6.	Dorsal spots on seventh and eighth abdominal segments	None.
7.	Anal plate	None.

Prepupa: Ordinarily as soon as the larva is fully fed, it enters the ground to spend the prepupal and pupal periods. During this time it shrinks, becomes more deeply yellow and in the last two or three days becomes strongly arcuate and unable to move.

As the larva moves about on the ground preparatory to entering the soil, it is very careful to choose a spot in which the soil particles are fine and preferably a little moist. It pushes its way down through the soil for a distance slightly less than an inch, and there by the twisting and turning of the body, and by a secretion, probably from the salivary glands, forms an ovate cell.

Pupa: (Fig. 1). The prepupa molts to the pupa ordinarily on the 7th day, and the cast skin is found in the cell. The pupa itself lies ventral side uppermost. The length is 2.93 mm., the greatest width 1.84 mm. The color is pale yellow and the general appearance is typically Chrysomelid.

During the first half of the period the pupa is quite active; when disturbed, by flexing its abdomen can change its position considerably. About the 4th day the eyes begin to darken and thereafter, legs, mouthparts and true wings. The elytra do not darken during the pupal stadium. The adult emerges on the 8th or 9th day after the prepupal molt, fully formed, light in color, inactive and still in the ground. In a few hours the elytra, head and thorax darken and finally the under

parts. The adult appears above the ground about 24 hours after emerging and begins feeding immediately.

Adult: (Fig. 1, Length, 3mm., Horn 1889). When the beetle first emerges from the pupal skin, it is as yellow in color as the pupa was. The legs and mouth parts are dark, the wings grayish, while the elytra and the under surfaces are pale yellow and slightly irridescent. Coloration takes place gradually; the upper parts become bronzy green in about twelve hours. Twelve more hours elapse before the under parts are fully colored. The beetle does not make its way above the ground until fully colored, although when disturbed it is able to move about and even leap characteristically.

The females appear to be slightly broader and the males more perfectly oval and seem to have a higher metallic lustre. However it is practically impossible to distinguish the sexes.

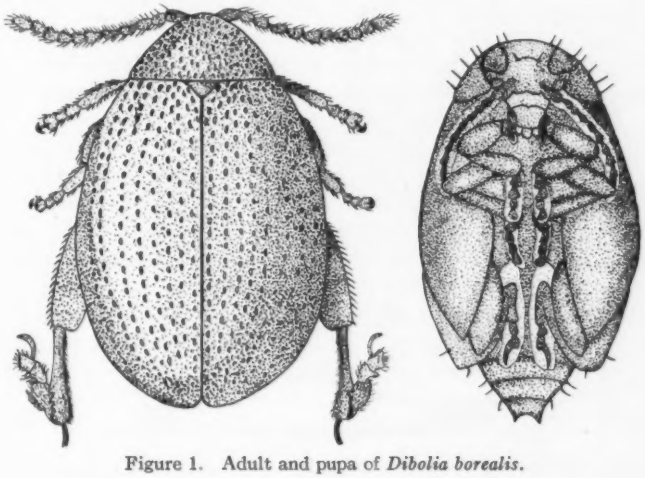


Figure 1. Adult and pupa of *Dibolia borealis*.

Activities of the Plantain Flea-beetle.

Feeding habits of larva: As already stated, the larvæ live within a mine, which they enter directly from the egg. Here with the two epidermal layers as shelter they are surrounded by an abundant food supply. When first formed the mine is very shallow and hard to distinguish; but few cells of the palisade layer are eaten. After the first molt, the larva feeds more deeply, removing the palisade and most of the spongy layers. After the second molt the entire space between the two epidermal layers is consumed (Fig. 2-z).

The mine is linear in form, though the larva frequently turns about feeding as it does so, and thus forms blotches along the way. Quite commonly, the larva makes a mine, then retraces its course and makes a side branch to it. Usually the larva prefers not to cross a large vein in the leaf, instead will often follow the course of the vein for considerable distance, and finally form a branch in the other direction. The surface of the leaf is "humped up" by the larva in its quarters, quite a characteristic habit of this miner. Frass is deposited in a mid

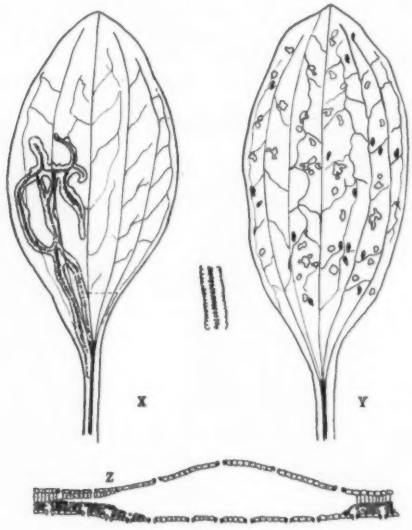


Figure 2. Infested leaves of *Plantago major*. X, Leaf showing mining operations of one larva; Y, Leaf showing eggs and feeding scars of adult; Z, Diagram of cross-section of a leaf showing depth of mine.

furrow in the mine. The edges of the mine appear to be "scalloped." (Fig. 2-x). This is due to the characteristic feeding habits. The larva holds its body stationary as it feeds, while the head is moved from side to side, until all the cells within reach have been devoured. Then the body is pushed forward and the whole process is repeated.

If the leaf becomes dried or too densely populated, the larva will leave, wander about on the surface of the leaf and eventually re-enter a new and fresher area or even a new leaf

if close at hand. A slit greater than the width of the larva is made in the upper epidermis and the larva slips under it, feeding as it does so.

Newly hatched larvæ will re-enter and mine the leaves of the narrow leaved plantain, though they never apparently choose it under natural conditions.

There is but one tenant in the mine, although there may be as many as five, six or seven healthy miners on a single leaf, each following its own course, and each reaching maturity.

Feeding habit of the adult: Directly after the adults have emerged, they begin to feed actively removing practically all of the upper epidermal palisade and spongy cells of the broad leaved plantain. The areas eaten out are small, frequently as small as the areas where the eggs are to be laid (Fig. 2-y). After a number of beetles have been feeding on a leaf for several hours, as in a breeding cage, the leaf assumes a lace-like appearance, dotted with black spots of excrement.

Adults are frequently found feeding on the under surface of the leaf, in this case leaving only the upper epidermis.

On cold, cloudy or wet days during May and June, the adults are very inactive and are found at the bases of the petioles of the leaf where they are somewhat sheltered. On a cold, damp morning therefore adults were easily caught. On a warm, sunshiny day when the beetles are busily engaged in feeding on the blades of the leaves, the little creatures leap at the slightest stirring of the vegetation, and are as elusive as true fleas.

The larger open holes of the plantain leaves are the feeding scars of some other insect, for none of these beetles observed in the laboratory made a scar even approaching the size often seen, in which both the epidermal layers are eaten as well as the cells between.

Copulation: Males and females were frequently seen and caught in copulation. In a mating pair caught and kept in captivity copulation was twice observed. It is possible that mating occurred previous to their capture and at other times in the laboratory when not observed.

Number of eggs: The egg complement is not all deposited at one time; egg laying covers a considerable period. Under natural conditions the female lays but few eggs on a leaf. All

the leaves of a plant in a breeding jar were literally covered by feeding scars and eggs from a single pair.

Natural enemies: Larvaæ in the field as well as in the laboratory are attacked by some kind of fungus. Apparently the conditions most favorable to their growth were present in Ithaca during late June and early July, for many larvæ were found dead in the mines from this infestation.

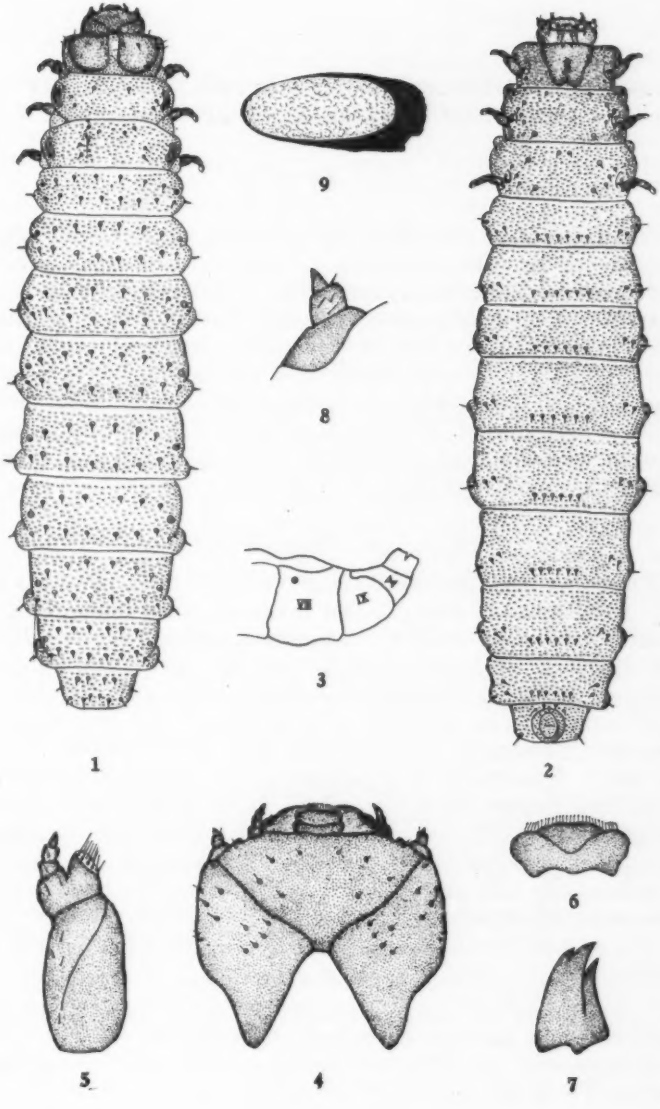
The larvæ of this beetle are unusually free from parasites. On one occasion however, two Hymenopterous larvæ were found in the mines on two different leaves.

BIBLIOGRAPHY.

Beutenmuller, William. 1890. Food Habits of the Chrysomelidae. Entom. Amer. 6:175.
1891. Bibliographical Catalogue of the Described Transformations of N. A. Coleoptera. N. Y. Micro. Soc. Journal VIII, 7:1-52.
Chevrolat. 1844. F. E. Guerin. Inconographie Regne Animal de G. Cuvier. p. 307.
Comstock, J. H. 1879. Report U. S. Dept. Agric., p. 248.
Gibson, Arthur. 1913. Can. Dept. Agric. Ent. Cir. 2, p. 6.
Horn, George Henry. 1889. Trans. Am. Ent. Soc. V, 16:163-320.
Lintner, J. A. 1895. Tenth Report of N. Y. State Entomologist, p. 414.
Melsheimer. 1847. Proc. Acad. Nat. Science Phila., III, p. 167.
Osborn, Herbert. 1891. Insect Life IV, p. 198.
Patch, E. M. 1908. Maine Agric. Exp. Sta. Bulletin 62:359, 1908.
Scudder, Samuel H. 1878. Psyche II, p. 154.
Woods, William C. 1917. Biology of Alder Flea-Beetle. Maine Agric. Exp. Sta. Bulletin 265, p. 249.

EXPLANATION OF PLATE XXVII.

Fig. 1. Grown larva of *Dibolia borealis*. Dorsal view.
Fig. 2. Grown larva of *Dibolia borealis*. Ventral view.
Fig. 3. Side view of larva showing 10th segment.
Fig. 4. Head. Dorsal view.
Fig. 5. Maxilla.
Fig. 6. Labrum.
Fig. 7. Mandible.
Fig. 8. Antenna.
Fig. 9. Egg, with excrementitious envelope.



Helen Reed

FURTHER OBSERVATIONS ON THE OLFACTORY POWERS OF THE NECROPHORI.

C. E. Abbott.

In June, 1927, I published a paper giving the results of some experiments on the olfactory peculiarities of *Necrophorus americanus* and *Necrophorus orbicollis*. These results left one question only partially answered, and raised another of some importance. The first related to olfactory threshold; the second to the possible olfactory function of the palpi. During July of the past summer I had at my disposal the Zoology laboratories of the University of Wisconsin. The nearby woods yielded about fifty specimens of N. orbicollis. These furnished sufficient evidence for the conclusions given here.

Olfactory Threshold.

The following tests were made with solutions of skatol in very pure distilled water. The dilutions were made with a burette, and were measured as grams per 100 c.c. of H_2O. The dilutions used were .00833, .00333, .0008, and .00024. Sheets of four-ply towelling measuring 4 x 4 inches were saturated with solutions and buried in the cage. In most cases a control, consisting of a similar pad wet with distilled water, was used. The results of experiments were considered positive if the test papers were unearthed, or if beetles were found beneath them. The tests were performed in the cage in which the beetles were kept; a wooden box 12 x 18 inches and about 12 inches deep. It was half filled with sand. The time factor, while not very constant, was usually about twelve hours.

The results of these experiments may be summarized as follows:

Experiment 1. A saturated solution of skatol was used. Of the sixteen beetles in the cage, fifteen went under the test paper.

Experiment 2. A .00833 solution was used with twenty-eight beetles. The results were entirely negative.

Experiment 3. A .00833 solution; and twenty-seven beetles were tested. Two were found under the test paper.

Experiment 4. A .0008 solution; and twenty-seven beetles were tested. No control was used. Twenty beetles were found under the test paper.

Experiment 5. A .0008 solution was used, and twenty-seven beetles were tested. The control paper was buried under a spot where some meat had been lying for several hours. The beetles unearthed both the test paper and the control in a single night, and chewed them very much. When supplied with meat, these beetles attacked it voraciously.

The four remaining experiments, employing .00024 skatol solutions, gave completely negative results.

The Palpi.

These experiments were performed in a regular insect breeding cage such as is often used for caterpillars. It was about 18 inches high and 12 inches square, and was filled to a depth of two inches with sand. A piece of meat was fastened at the top of two alternately inclined planes. Of the twenty beetles in the cage, ten had amputated palpi, and were so marked that they could be easily distinguished from the normal insects.

The results were as follows:

On July 11th two normal beetles were feeding on the meat.

On July 12th two normal beetles and three without palpi were feeding.

On July 13th four normal beetles and five without palpi were feeding.

On July 14th two normal beetles were feeding.

The meat was then removed from the plane and suspended from the top of the cage so that it was a few inches above the sand. In this position even normal beetles would not respond to it, and so it was put at the top of a single inclined plane. On July 17th two beetles, one without palpi, were found on the meat. The following evening a single beetle with amputated palpi was feeding.

At this point general tests were discontinued, and a few beetles were tested with essential oils. Normal insects were used as controls. The method was to bring a bit of wood saturated with the test substance within a few millimeters of the beetle's head. If the insect did not move within sixty seconds the response was considered negative.

Individual	Condition	Test Substance	Response	Reaction Time
I (tomentosus)	normal "	bergamot wintergreen	+ +	immediate 5 seconds
II (orbicollis)	no palpi " "	bergamot wintergreen	+ ?	10 seconds
III (orbicollis)	" " " "	bergamot wintergreen	+ +	immediate 10 seconds
IV (orbicollis)	" " " "	bergamot wintergreen	+ —	5 seconds
V (orbicollis)	normal "	bergamot wintergreen	— —	
VI (orbicollis)	no palpi " "	bergamot wintergreen	+ +	20 seconds 5 seconds
VII (orbicollis)	normal "	bergamot wintergreen	+ +	30 seconds 8 seconds
VIII (orbicollis)	no palpi " "	bergamot wintergreen	+ +	45 seconds 8 seconds

General Considerations.

It is strange that the results obtained relating to the olfactory threshold of the Necrophori differed so much from those obtained in the summer of 1926. The difference was in some way related to the behavior of the two groups of beetles. Those used in the recent experiments were always restless and hungry; it was impossible to satisfy them. Moreover, for some inexplicable reason, great numbers of them sometimes died over night. None of these phenomena were observed the summer before. They must be related to factors which are not yet well understood. The data obtained in the two cases do not invalidate each other, but it is evident that neither can be wholly accepted without further confirmation.

The results relating to the palpi were more gratifying. Vision can be eliminated as a factor in these experiments. Former tests have convinced me that the visual powers of the Necrophori are not particularly good. The very fact that the beetles are nocturnal, and work in almost absolute darkness, sufficiently demonstrates the importance of the olfactory sense.

After considering these reservations, it is quite certain that the palpi have very little, if anything, to do with olfaction. This enables me to state my position once more: I cannot understand how the olfactory organs of the Necrophori can be localized, and the only alternative conception is a general distribution over the surface of the body. In view of the evidence, the generalizations of von Frisch (1921) seem premature.

BIBLIOGRAPHY.

Abbott, C. E. 1927. Ann. Entom. Soc. Am., 20:2.
Frisch, K. von. 1921. Uber den Sitz des Geruchsinnes bei Insecten. Zool. Jahr., 53.

THE DEVELOPMENT OF COCCOPHAGUS GOSSYPARIÆ GAHAN, A PARASITE OF THE EUROPEAN ELM SCALE.

GRACE H. GRISWOLD,
Cornell University.

While working on the biology of the European elm scale (*Gossyparia spuria* Modeer) during the spring of 1924 some males were found that appeared to be parasitized. This condition was first noticed while the male coccids were still in the second larval stage although their cocoons had already been formed. Upon dissecting some of the parasitized individuals each was found to contain a pale cream-white hymenopterous larva, apparently about ready to pupate. Their feces had been voided and lay about them in the form of flat black plates. In order to get an idea of the percentage of parasitism counts were made of a number of males. An examination of 163 coccids showed that 47 (28.83%) of them were parasitized. A few days later hymenopterous pupæ were dissected from some of the male coccids. Measurements of a number of these pupæ showed them to be about 1.2 mm. in length and 0.54 mm. in width. The general color of the pupa is black although the thorax and the abdomen are slightly lighter than the head and have a somewhat greenish tinge. On the ventor, the thorax and the abdomen are much lighter, the latter being a pale greenish-white but with a dark area at the caudal end. It

was noticed that the pupa usually lies with its head at the posterior end of its host's body though some were found in a reverse position.

The first adult parasites emerged in vials on May 19th and they continued to emerge for nearly two weeks. Each had cut a neat round opening in the body of its host and a second opening in the host's cocoon. The exit hole was usually found to have been made near the center of the dorsum although in a few instances exit holes were found at one end of the coccid's body. Specimens of the chalcids were sent to Washington for determination and have lately been described by Gahan (1927: 24) as *Coccophagus gossypariæ*. Cooley (1898:63) reared a parasite from the European elm scale and sent specimens to Washington to have them identified. Dr. Howard found them to be a new species to which he gave the manuscript name of *Coccophagus gossypariæ*. No description, however, was published at that time. The parasites reared in the present study were compared by Gahan with the Cooley specimens and found to be the same. Gahan in his recent description of the species has retained the name given the insect by Dr. Howard in 1898.

At about the time that the parasites began emerging the mature female coccids had settled on the twigs and started their semi-cocoons. An effort was made to get the chalcids to oviposit in some of these individuals. Bits of twigs on which the scale insects had settled were put in small vials into which parasites were also inserted. The parasites showed great interest in the coccids, walking back and forth over them and tapping them with their antennæ. Later on, however, when the coccids were removed from the vials and dissected no eggs could be found.

In late June coccid females from five different elm trees were dissected for the presence of parasites. The total number of scale insects so examined was 316 and of these 94 (29.77%) were found to be parasitized. Some of the parasites were tiny larvæ, others more fully developed and still others had pupated. A full grown chalcid larva of the second generation is larger than one of the first generation, probably due to the greater amount of food supply afforded. It occupies a U-shaped position in the body of its host which by this time is nothing but a hollow shell.

When ready to pupate the larva gives off its excrement, straightens out and lies at one end of the host's body. The pupa may lie with its head at the cephalic end of its host or in a reverse position or it may lie slantwise. As in the case of the larvæ, the pupæ of the second generation are somewhat larger than are those of the first generation, but otherwise no difference was noted.

The first chalcid adults emerged in vials July 9th. In order to avoid any possibility of error, specimens were sent to Washington for determination. They proved, however, to be the same species as those which had begun to emerge from male coccids six weeks before.

It is evident, therefore, that there are at least two generations a year of this parasite. The first generation parasitizes the male scale insects before they have fully matured. The second generation, on the other hand, attacks the Gossyparia females. The adults of this second generation emerge at about the time that the eggs of the scale insect are hatching. At Ithaca *Gossyparia spuria* has only one generation a year and passes the winter in the second larval stage. The manner in which the parasite over winters is yet to be determined.

REFERENCES CITED.

Cooley, R. A. U. S. Ent. Div. Bul. 17, n. s. :61-65. 1898.
Gahan, A. B. No. 2676, Proceedings U. S. National Museum, vol. 71, art. 4, pp. 1-39. 1927.

INDEX TO VOLUME XX.

Abbott, C. E., articles by, 117, 207, 550.
Acinopterus, New Species of, 232.
Agromyzidæ, 217.
Alexander, C. P., article by, 301.
Allee, W. C., article by, 439.
American Catopsilias, 474.
Amphibolothrips grassii, 8.
Anatomy of the larva of Hoplocampa halcyon, 481.
Anastatus albitarsis, Bionomics of, 461.
Andrena, 396.
albihirta, 396.
eriogoni, (Trachandrena), 397.
lewisii, 397.
topazana, 397.
Anomala Kansana H. and McC., Immature Stages and Larval Anatomy of, 193.
Anthonomus vestitus, 251.

Aphis Gossypii, The Variability of, 263.
Aphis, 344.
helianthi, 346.
oenotheræ, 344.
oenotheræ rufa, 346.
oestlundi, 345.
Aphid Species and the Genus Illinoia Wilson, 344.
Aspidiotus socialis, 349.
Augochlora holti, 397.
viridilustrans, 398.

Ball, E. D., articles by, 419, 488.
Batchelder, C. H., article by, 263.
Beal, J. A., article by, 522.
Bebelothrips, 5.
latus, 6.
Bionomics of Anastatus albitarsis, 461.
Bionomics, Insect, 436.
Bees, North and South American, 393.
Bird, Ralph D., article by, 481.
Bradythrips, 4.
hesperus, 4.
Bremidæ, 156.
Bruchus quadrimaculatus Fab., The Host-Selection Principle as Applied to, 37.
Byers, C., article by, 385.
Bumblebees, Development of Castes of, 156.
Hibernation of, 181.

Calliphoridæ, 368.
Canifa plagiata millikini, 366.
Castes of Bumblebees, Development of, 156.
Catopsilia, 474.
agarithe, 476, 478.
argante, 478, 479.
avellanada, 475, 478.
boisduvallii, 477, 479.
cipris, 476.
etiolata n. sp., 477, 479.
eubule, 476, 479.
godartiana, 477, 479.
jada, 477, 479.
jaresia, 479.
hartonii, 477, 479.
hersilia, 476.
intermedia, 478.
menippe, 477, 478.
neocipris, 478.
neleis, 479.
orbis, 479.
philea, 475, 478.
rotata, 479.
rurina, 476.
sennæ, 476, 479.
statira, 477, 479.
thalestris, 475, 478.
trite, 478.
virgo, 479.
wallacei, 479.
Catopsilias, American, 474.
Ciliated Epithelium in the Insecta, 359.
Clausen, Curtis P., article by, 461.
Cluster Fly Pollenia Rudis (Fab.), A Bionomical Study of, 368.
Coccophagus gossypariæ, Development of, 553.
Cockerell, T. D. A., article by, 393.
Coleoptera, Experimental Data on the Olfactory Sense of, 207.
Computing of Mean Temperatures for Biological Use, 255.
Control Measures, 454.
Cotton, R. T., article by, 81.
Crane-Flies of Mexico, Studies on, 301.
Crypthemichionaspis ulmi, 350.
Crytolabis luteiceps, 315.
Cutright, C. R., article by, 255.

Davis, A. C., article by, 359.
DeCoursey, R. M., article by, 368.
Diadasia diminuta, 400.
Diaspines from Mississippi, Some Undescribed, 349.
Dibolia borealis, Observations on, 540.
Dicranomyia exaeta, 305.
Dione Vanillæ, On the Seasonal Migrations of, 242.
Diotrepha mirabilis Osten Sacken, Notes on the Life History, Distribution and Ecology of, 23.
Doane, R. W., article by, 436.
Dolichopodidæ, 123.
Dragonana n. g., 489.
Dragonana dracontia, 490.

Ecitor Schmitti Emery, 401.
Ecology, Insect, 439.
Economic Entomology, 451.
Enallagma and Telagrion from Western Florida, 385.
Enallagma, 385.
cardenium, 392.
civile, 392.
concisum, 392.
cyathigerum, 392.
daeckii, 392.
divagans, 389.
doubledayi, 392.
dubium, 388.
durum, 392.
geminatum, 389.
laurenti, 388.
pallidum, 389.
pollutum, 388.
signatum, 388.
sulcatum, 388.
traviatum, 389.
versperum, 392.
weewa, 385.
Ephemerella, Rocky Mountain Species of the Mayfly Genus, 107.

Ephemerella, 107.
coloradensis, 113.
dodsii, 111.
grandis, 108.
hecuba, 115.
inermis, 114.
margarita, 114.
spinifera, 110.
Erioptera, 309.
apicinigra, 313.
dampfi, 311.
leucopasta, 313.
modica, 314.
oresitropha, 310.
quadricincta, 310.
saturata, 312.
stygia, 309.
Essig, E. O., article by, 451.
European Corn Borer, a Contribution to the Study of Hibernation in the Larva of, 10.
Ewing, H. E., article by, 245.
Exomalopsis, 400.
giacomellii, 400.
torticornis (Anthophoru), 399.

Filterable Viruses, Studies on the Polyhedral Diseases of, 319.
Fink, D. E., article by, 503.
Flint, W. P., article by, 454.
Forbes, W. T. M., article by, 474.
Formica dakotensis specularis, Effect of Monochromatic Light on, 117.
Frison, T. H., article by, 156.
Frost, S. W., article by, 217.

Giant Thorn-Headed Worm of Swine, Another Intermediary Insect Host of, 86.
Gillette, C. P., article by, 344.
Glaser, R. W., article by, 319.
Glasgow, Robert D., articles by, 86, 127.
Griswold, Grace H., article by, 553.
Gonomyia, 306.
chiapasensis, 306.
maya, 307.
Gypona and Its Allies, Further Studies on, 488.
Gypona signoreti, 494.
unicolor, 494.
verticalis, 495.
Gyponana chadana, 493.
octolineata, 490, 493.
var. cana, 491.
pruinosa, 492.
striata, 491.
tenella, 492.
rugosa, 493.

Halictus perater, 396.
Hatch, M. H., articles by, 363, 366.
Hayes, Wm. P., article by, 193.
Heptagenia Interpunctata, Malpighian Tubules of, 149.
Hinds, W. E., article by, 251.
Hippoboscid Fly, as a Carrier of Mallophaga, 245.
Hoke, Gladys, article by, 349.
Hood, J. Douglas, article by, 1.
Howard, L. O., article by, 445.
Hoplocampa halcyon, Anatomy of, 481.
Host-Selection Principle, 37.
Hungerford, H. B., article by, 262.
Hydrogen Ion Concentration, Application of in Entomological Research, 503.
Hydrometra, A New Species from North America, 262.
Hypanthidium flavomarginatum, 394.

Ichneumonids of the Genus Paniscus Schrk, Biology of, 405.
Illinoia, 347.
Insects Beneficial, 445.
Insect Bionomics, 436.
Insect Ecology, 439.
Insect Physiology, 429.
Insect Vector of the Giant Thorn-headed Worm of Swine, 127.

Kennedy, C. H., article by, 87.
Knight, Harry H., article by, 224.
Knowlton, George F., article by, 229.

Langston, J. M., article by, 221.
Larson, A. O., article by, 37.
Lawson, Paul B., article by, 232.
Legionary Ants, Biology and Distribution of, 401.
Lepidosaphes ilicis, 352.
solidaginis, 354.
Limonia, 303.
infuscata, 303.
ludibunda, 304.
perflaveola, 304.

Macrosiphum pisi, 348.
Malachiinæ, 366.
Mallophaga, 245.
Malpighian Tubules of Larva of Heptagenia Interpunctata, Say, 149.
Marshall, Wm. S., article by, 149.
Meal Worms, Notes on the Biology of, 81.
Mean Temperatures, Computing of for Biological Use, 255.
Megachile, 395.
hoffmannseggiæ, 395.
hoffmannseggiæ hypoleuca, 395.
jurujubensis, 394.
Megalopsallus, New Genus, Miridæ, 224.
Melandrya, 364.
(Emmesa) blackmani, 364.
colorata, 365.
(Neoemmesa) noveboracensis, 365.

Melandryidæ, Concerning, 363.
Melissodes lavata, 395.
Miridæ, a New Genus of, 224.
Molophilus, 316.
  fuscopleuralis, 317.
  obediens, 316.
  pennatus, 318.
Myers, J. G., article by, 279.

Necrophori, Olfactory Powers of, 550.
Necrophori, Olfactory Sense, 207.
Needham, James G., article by, 107.
North American Bumblebees, Notes on Hibernation of, 181.
North American Polymedon, 123.
North and South American Bees, 393.

Observations on Pyrrhocoridæ of Cuba, 279.
Olfactory Powers of Necrophori, 550.
Olfactory Sense of Coleoptera, Experimental Data on, 207.
Ornithomyia Avicularia Linnaeus, 245.

Paniscus Schrk., Biology of Some Ichneumonids of, 405.
Parker, H. L., article by, 10.
Peruvian Cotton Square Weevil, Notes on the Biology and Habits of, 251.
Phillips, E. F., article by, 457.
Phyllophaga from Mississippi, New Species of, 221.
Phyllophaga vehemens, 86.
Physiology, Insect, 429.
Phytomyza, Three New Species of, 217.
Phytomyza langelicella, 218.
  auricornis, 217.
  marginalis, 219.
Pityogenes hopkinsi, 522.
  Proventriculus of, 522.
Plath, O. E., article by, 181.
Polyhedral Diseases of Insects Due to Filterable Viruses, 319.
Ponona resima, 499.
  scarlatina, 497.
    var. dohrni, 498.
      citrina, 398.
      grisea, 498.
      irrorella, 498.
      limbatipennis, 498.
      limonea, 498.
      meditabunda, 498.
      pauperata, 498.
      pectoralis, 498.
      puncticollis, 498.
      rodora, 498.
      scarlatina, 498.
      sanguinolenta, 498.
Prairiana cinerea, 495.
  var. moneta, 496.
    orizaba, 496.
Proceedings of the Twenty-first Annual Meeting, 131.
Pyrausta nubilalis, 10.
Pyrrhocoridæ, Ethological Observations on, 279.

Rabbit Brush Aphid from Utah, 229.
Randolph, Vance, article by, 242.
Reed, Helen, article by, 540.
Reeves, J. A., article by, 488
Rhabdomastix isabella, 315.
Robinson, Wm., article by, 513.
Roger, J. Speed, article by, 23.
Rohwer, S. A., article by, 423.

Seasonal Migrations of Dione Vanillæ in Kansas, 242.
Sensitivity of Insects to Moisture, Temperature, Light and Odors, 87.
Smith, M. R., article by, 401.
Stephanothrips, buffai, 6.
  occidentalis, 6.
Symposium: Needed Lines of Investigation in American Entomology, 419.
Symposium Summary, 457.

Taxonomy, 423.
Telagrion from Western Florida, 385.
Temnopsophus and Pseudebaeus, New Abberrations of, 366.
Tenebrio molitor, 81.
  T. obscurus, 81.
Teucholabis dampfi, 308.
Thermocouple Method of Determining Temperatures, 518.
Thompson, W. R., article by, 10.
Thysanopterous Family, a Synopsis of, 1.
Tipuloidea, 301.

Urothripidæ, 3.
Urothripoidea, 2.
Urothrips, 3.
  bagnallis, 4.
  paradoxus, 3.
Urothripidæ, a Synopsis of the Thysanopterous Family, 1.

Vance, Arlo M., article by, 405.
Van Duzee, M. C., article by, 123.
Vector of the Giant Thornheaded Worm of Swine, 127.

Welch, P. S., article by, 429.
Williams, C. B., article by, 1.

Xerophloea, 489.
Xyloryctes satyrus, 127.

MARVEL